TAXONOMIC REVIEW OF THE AUSTRALIAN ROSSIINAE (CEPHALOPODA: SEPIOLIDAE), WITH A DESCRIPTION OF A NEW SPECIES, *NEOROSSIA LEPTODONS,* AND REDESCRIPTION OF *N. CAROLI* (JOUBIN, 1902)

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ABSTRACT

Geographical variation in the morphological characters of Australian Rossiinae were examined using principal component analysis (PCA), multivariate analysis of variance (MANOVA), discriminant function analysis (DFA), analysis of variance (ANOVA) and latitudinal and longitudinal regression analyses. The results show that morphological differences occur between populations of *Rossia* from the North West Shelf (W.A.) and populations from eastern and southern Australia. Evidence from these analyses suggest that these two populations are genetically distinct, the North West Shelf specimens belonging to a possible new species, described as *R.* sp. 1, the eastern and southern Australian specimens identified as *R. australis* Berry, 1918 and redescribed on the basis of new material. That all the latter specimens belong to a single species is further supported by electrophoretic evidence. A new species of *Neorossia, N. leptodons,* is identified and described, differing from the only described representative of this genus, *N. caroli* (Joubin, 1902), in the shape of the radular teeth. The two species were also shown to differ using multivariate statistical techniques. *N. caroli* is redescribed from the holotype and additional material. In addition, specimens of *Neorossia* from southeastern Australia are compared electrophoretically with *R. australis.* It was found that members of these two genera differed for 66% of loci.

The Rossiinae are a group of relatively small (up to 10 cm mantle length) sepiolids found circumglobally on continental shelves and upper slopes. There are three currently recognized genera in the Rossiinae; *Semirossia* Steenstrup, 1881; *Neorossia* Boletzky, 1971 and *Rossia* Owen, 1835. *Rossia* is furthur divided into two subgenera, *Rossia* and *Austrorossia* Berry, 1918.

Semirossia is characterized in having only the right dorsal arm hectocotylized and by the presence of a light organ on the ink sac (Boletzky, 1970). Anal valves and the ink sac are well developed in this genus. Three species of *Semirossia* have been recorded from the eastern coast of America; from Nova Scotia to Tierra del Fuégo and southern Chile (Nesis, 1987). To date, no species of *Semirossia* have been recorded from Australia. In the other two genera, *Neorossia* and *Rossia,* both dorsal arms of males are hectocotylized. *Rossia* has a functional ink sac and well developed anal valves, while in *Neorossia* they are vestigial.

The genus *Rossia* was erected to accommodate a new species collected in the Canadian Eastern Arctic during the Ross expedition (Owen, 1835). The genus is widely distributed, with seven species currently recognized in the Atlantic, one species found in the Arctic and six species from the Indo-Pacific.

Only one species, *R. australis* Berry has been recorded from Australia. In describing this species, Berry (1918, 252) erected the subgenus *Austrorossia,* distinguishing it from the remaining *Rossia* as follows: "1) The tentacular club is unusually long, more or less coiled and armed with an immense multitude of infinitesimal suckers. 2) The suckers on the sessile arms are in two rows throughout. 3) Some of the suckers on the sessile arms of males suffer sexual modification ie., enlargement. 4) The hectocotylised arms of the males are characterized not only by the modification in the size of certain suckers as above, but (in the type

species at least) by the presence of a pocket-like gland on the outer surface of the arm."

This diagnosis has since proved to be inadequate. Only the first character can reliably be used to distinguish the two subgenera, with *Austrorossia* possessing 18–46 oblique rows of club suckers (this study) and *Rossia* 5–16 (Mercer, 1968). Characters 2–4 above apply equally to some members of the subgenus *Rossia*. Despite this difficulty, the subgenera have been maintained with additional characters used to support their separation. Distinguishing features of the subgenera *Rossia* and *Austrorossia,* based upon work following that of Berry (1918), are given by Nesis (1987, 122). There is still some overlap in characters between some species of the two subgenera based on this diagnosis. These have been discussed elsewhere (Reid, 1990). However, pending a comprehensive review of the entire genus, the subgeneric division of Nesis (1987) is followed here. Using his definition, species belonging to *Austrorossia* are: *R. antillensis* Voss, 1955; *R. australis* Berry, 1918; *R. bipapillata* Sasaki, 1920; *R. enigmatica* Robson, 1924; and *R. mastigophora* Chun, 1915. The subgenus *Rossia* includes: *R. brachyura* Verrill, 1883; *R. bullisi* Voss, 1956; *R. macrosoma* (Delle Chiaje, 1829); *R. megaptera* Verrill, 1881; *R. palpebrosa* Owen, 1835; *R. moelleri* Steenstrup, 1856; *R. mollicella* Sasaki, 1920 and *R. pacifica* Berry, 1911.

With respect to members of *Austrorossia,* Voss (1962, 254–255) states "only *R. antillensis* has been collected in sufficient quantity to permit analysis of ranges and variation. The subgenus is widely distributed and a strong possibility exists that they all represent merely geographical variants of a single species." The absence of clear morphological distinction between nominal species of *Austrorossia* lends some weight to this conclusion. This view is shared by Nesis (1987, 122–126), who states that differences between *Austrorossia* species are doubtful and suggested that *R. australis* was possibly a synonym of *R. mastigophora.* Voss (1962) and Nesis (1987) also questioned whether the two nominal African species *R. mastigophora* and *R. enigmatica* were distinct.

Only *R. bipapillata* can be easily separated from other species; it is unique within the subgenus in having epirenal bodies (glandular structures of unknown function which lie on either side of the kidney papillae) in both sexes. These are currently known to occur only in the males of the remaining species.

Conversely, members of the subgenus *Rossia* appear to be more adequately defined. Mercer's (1968) work on Canadian species of the subgenus *Rossia* showed them to have restricted distributions which he attributed to limitation placed on dispersal as a consequence of direct development of the young. This suggestion has also been noted by Mangold-Wirz (1963). However, given that all *Rossia* species appear to have similar dispersal capabilities, the differences between the reported distributions of species of *Rossia* (*Rossia*) and species of *Rossia* (*Austrorossia*) may be simple reflections of differing levels of resolution of species limits within the two groups. This explanation has been alluded to by Voss (1962) and in part provided the impetus for the present review.

Since the description of *Rossia australis* Berry (1918), a large number of *Rossia* have been collected from around the Australian coastline over a wide distributional range. Much of this material has been lodged with Australian museums and tentatively assigned to *R. australis.* Given the current poor understanding of the systematics of *Austrorossia* (Voss, 1962; Nesis, 1987), and considering the narrow distributions reported for Canadian species of *Rossia* (Mercer, 1968), a detailed examination of Australian specimens is justified.

In addition to *Rossia,* examination of furthur available specimens of the Rossiinae revealed several specimens of a second genus, *Neorossia.* Nesis (1979; 1987)

collected a single male specimen of *Neorossia* from the Great Australian Bight (33°49'S, 127°09.4'E–33°46'S, 127°27.3'E) (during the 16th cruise of the research vessel DMITRY MENDELEEV in 1976). The specimen, trawled from 1,100–1,080 m, was recorded as *N. caroli* by Nesis (1979; 1987). This species, the only member of the genus, was described as *Rossia caroli* by Joubin (1902) and subsequently placed in a new genus *Neorossia* by Boletzky (1971). *N. caroli* is reported from the northeastern Atlantic (southwestern Iceland and Ireland) to the Mediterranean Sea and southwestern Africa. Thus, the large range extention noted by Nesis (1979; 1987) for *N. caroli* raises questions about the correct identity of the Australian *Neorossia* specimens.

Comparisons were made between Australian *Neorossia* and *N. caroli* from the eastern Atlantic Ocean in order to clarify the systematic status of the Australian specimens.

A preliminary investigation of Rossiinae material showed that qualitative characters did not appear to differ markedly between specimens from a range of localities, so a statistical approach was employed to examine possible variation in quantitative (both meristic and morphometric) characters. Such characters were subjected to univariate and multivariate statistical analyses to determine any underlying pattern in the data matrix and to look for groups of phenetically related specimens. Secondly, the attributes of each group were tested to determine whether any detected groups were discrete and conformed to the assumptions of taxonomic species.

MATERIALS AND METHODS

Material Examined

This study is based mainly on museum collections. The material examined consists of type material (where possible), Australian specimens and selected species from other geographic areas. All material studied is listed in Appendix 1. Institutional acronyms used throughout this paper are: AMS—Australian Museum, Sydney, Australia; MOM—Musee Océanographique Monaco, Monaco-Ville, Monaco; MV—State Museum of Victoria, Melbourne, Australia; SAM—South Australian Museum, Adelaide, Australia; UMML—University of Miami, Florida, U.S.A; USNM—National Museum of Natural History, Washington, D.C., U.S.A. and WAM—Western Australian Museum, Perth, Australia.

Morphology.—ROSSIA. The analysis of geographic variation in *Rossia* was based on 272 specimens (227 females, 45 males) collected from the North West Shelf, Western Australia (18°40'S, 117°13'E to 13°25'S, 122°47'E) and from a range of sites extending from Raine Island, Queensland (11°35'S, 144°04'E) to the Great Australian Bight, Western Australia (34°S, 130°50'E) in depths ranging from 131–665 m.

The Australian *Rossia* were compared with 14 African specimens which had been identified as *R. enigmatica* (ten females) and *R. mastigophora* (one female, three males). As the *R. enigmatica* specimens could not be distinguished from *R. mastigophora* specimens from close to the type locality of *R. mastigophora* (0°27'S, 42°47'E), both in characters used by Robson (1924) in describing *R. enigmatica* and in additional characters examined in this study, all the available African specimens of *Rossia* were grouped and called *R. mastigophora* in the following analyses. A map showing sites of collection for African specimens examined in this study is given in Appendix 2.

NEOROSSIA. Sixteen female and three male *Neorossia* from southern and southeastern Australia (32°08'S, 153°07'E to 33°42'S, 132°25'E) were compared with nine female and seven male *Neorossia caroli* (including the holotype MOM 29-5136) ranging from the Mediterranean Sea (41°11'N, 02°27'E) to the Namibian coast of southern Africa (23°23'S, 13°13'E). Four male (SAM D18725 and SAM D18726) and one female (SAM D18724) Australian *Neorossia* were received at the time of writing. Descriptive data for males are included for these specimens; however, they were not included in multivariate analyses.

Electrophoresis.— Eight *Rossia* (one from the North West Shelf, four from western Tasmania and three from off Sydney) and four *Neorossia* (from western Tasmania) were compared electrophoretically. Specimens used for electrophoresis are indicated in Appendix 1.
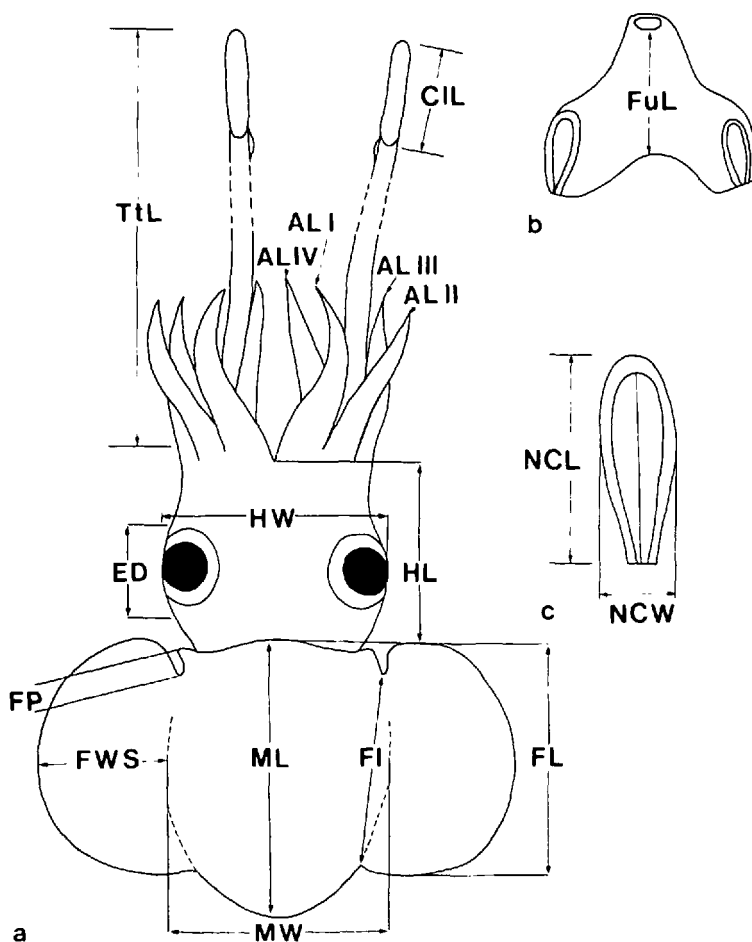
Figure 1. Diagram of measurements. a) Entire animal, dorsal view; b) Funnel; c) Nuchal locking cartilage.

Specimen Capture and Preservation. — Most Australian specimens were collected during fisheries surveys or as bycatch of prawn or orange roughy (*Hoplostethus atlanticus*) trawls. Trawl specifications have not been included here, however this information can be derived from station numbers listed in Appendix 1.

Specimens were either frozen then fixed, or fixed immediately in 10% formalin soon after capture and subsequently preserved in either formalin (Australian Museum specimens) or 70% alcohol (all other institutions). Specimens used for electrophoresis were frozen soon after capture aboard ship then stored at −80°C prior to preparation of tissue extracts. The time taken between capture and freezing at −20°C is not known. Two to four weeks elapsed after capture to the time frozen specimens were transferred to −80°C.

Character Descriptions and Abbreviations

Measurements and indices used throughout this paper are those given in Roper and Voss (1983), using dorsal mantle length (ML) as a size standard. Definitions of counts and measurements are given in Table 1 and most are illustrated in Figure 1. Indices were calculated by dividing each measure by ML. Some additional measures and counts have been used. Fin position (FP), fin insertion (FI) and single fin width (FWS) were used by Mercer (1968) and have been adopted for this study. Nuchal locking cartilage length and width (NCL and NCW respectively) were measured and ratios of fin length
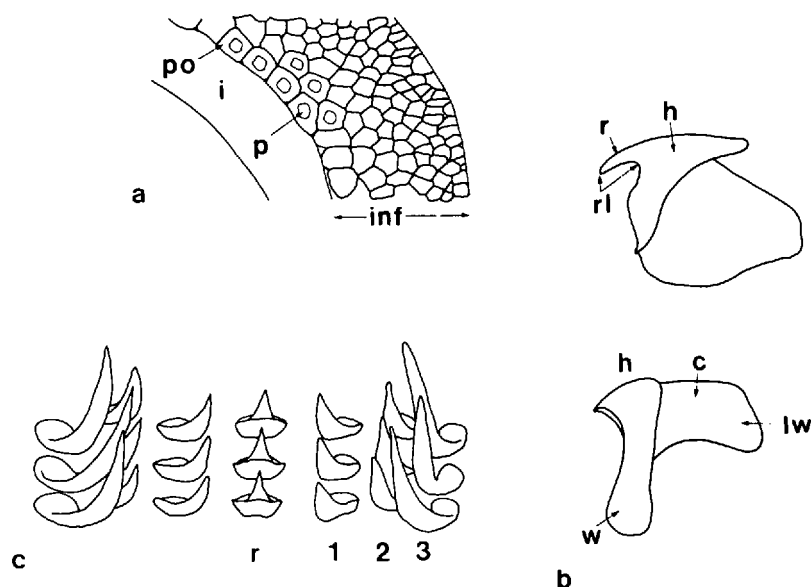
Figure 2.   Terminology—a) Arm sucker rim (inf—infundibulum, i—inner ring, po—polygonal process, p—peg); b) Beak (top—upper beak, below—lower beak), (r—rostrum, h—hood, rl—rostral length, c—crest, lw—lateral wall, w—wing); c) radula (r—Rhachidian tooth, 1—1st lateral tooth, 2—2nd lateral tooth, 3—3rd lateral tooth).

to width (FL/FW) and nuchal locking cartilage length to width (NCL/NCW) were calculated. The total number of suckers (ASCT) on each arm was counted for some specimens. Nidamental gland length (NDL) and width (NDW) in females were measured and compared with the development of the ovary. In this way, any mature females which may have spawned prior to capture could be detected. For internal anatomy, the terminology of Tompsett (1939) has been followed. Parts of club and arm sucker rims are described using the terminology of Nixon and Dilly (1977). Beaks were described following Clarke (1986). Arm sucker rims and beaks are illustrated and terminology explained in Figure 2a and b. (Terminology for club sucker rims is the same as for arm sucker rims.)

Gladius length was not measured because of the difficulty in removing the entire gladius intact from a sufficient sample of specimens and the resultant damage to specimens necessitated by such removal.

The number of specimens used in the analysis of morphometric and meristic data varied, as some specimens were partially distorted and/or damaged. For example, gill lamellae were often damaged and torn probably as a result of trawling and counts of these could not be made for many specimens. Tentacles were often broken off, thus club sucker row counts could not be made for all material.

Most measurements were made using dial callipers and expressed to 0.1 mm accuracy. Arm and club sucker diameter were measured using an eyepiece graticule attached to a stereo microscope. Club sucker diameters were expressed to 0.01 mm. Arms were often bent in such a way to make measurement with callipers difficult and inaccurate, so arm lengths were measured using a piece of fine cotton thread later measured against a metal rule.

Tentacle length, though measured, was not included in statistical analyses as this structure is most prone to stretching and distortion, making measurements unreliable for comparison.

Scanning Electron Microscopy

Arm suckers from the fourth sucker row from the base of each arm (4 per specimen) and club suckers from the middle portion of the club (10 per specimen) were removed from 15 specimens from a range of localities to compare structure. After removal from specimens, arm and club suckers were dehydrated in an ethanol series.

Radulae were dissected from the buccal mass, soaked for several hours in a 5% potassium hydroxide solution then cleaned with a sonic cleaner and a fine probe. In all cases the new, unused portion of the radula was examined.

All prepared material was air dried, mounted, coated with gold and examined in a JSM 840 (Japan

Table 1. Description of measurements and counts (characters used in PCA are underlined in bold)

AF	Arm formula: comparative length of arms expressed numerically in decreasing order, e.g., III.II.IV = 1.	**FWT**	Total fin width: greatest width (dorsally) across both fins.
AL	Arm length: length of first arm measured from first basal sucker to tip of arm. (Arm I, dorsal; II, dorso-lateral; III, ventro-lateral; IV, ventral).	**FuL**	Funnel length: length of funnel from the anterior opening to the posterior border measured along the ventral midline.
AS	Arm sucker diameter: diameter of largest sucker on each designated arm.*	GiLC	Gill lamellae count: number of lamellae on outer demibranch excluding the terminal lamellae.
ASC	Arm sucker count: number of suckers on basal half of each designated arm.	**HL**	Head length: dorsal length of head measured from point of fusion of dorsal arms to anterior tip of nuchal locking cartilage.
ASCT	Arm sucker count: number of suckers (or where missing, sucker pedicles) on each designated arm.	**HW**	Head width: width of head at the level of the eyes.
ClL	Club length: length of club measured from proximal-most sucker to distal tip of club.	ML	Dorsal mantle length: measured from anterior-most point of mantle to posterior apex of mantle.
ClRC	Club sucker row count: number of oblique (with respect to the longitudinal axis of the club) rows of suckers across the width at the midpoint of the club.	**MW**	Mantle width: greatest straight line (ventral) width of mantle.
ClS	Club sucker diameter.†	**NCL**	Nuchal cartilage length: measured at the dorsal midline.
ED	Eye diameter: diameter of eye across bulbus.	**NCW**	Nuchal cartilage width: greatest width of cartilage.
EgD	Egg diameter: diameter of largest egg present in the ovary or oviduct.	NDL	Nidamental gland length: greatest length of gland.
FI	Fin insertion: length of fin as joined to the mantle.	NDW	Nidamental gland width: greatest width of gland.
FL	Fin length: greatest length of fins.	SpL	Spermatophore length.
FP	Fin position: distance from the anterior margin of fin insertion to anterior mangle margin.	SpW	Spermatophore width.
		TtL	Tentacle length: total length of tentacle stalk and club measured from point of emergence of tentacle level with arm web, to distalmost tip.
FWS	Single fin width: greatest width across a single fin from its ventral junction of the mantle.		

* Roper and Voss (1983) give this measure as the diameter of the largest normal arm sucker as distinct from enlarged arm suckers that occur on the hectocotylized arm pair I in *Rossia*. In this study, the largest sucker was measured for each arm irrespective of nature of enlargement.
† Suckers measured at the midpoint instead of largest sucker as used by Roper and Voss (1983).

Electron Optics Ltd. Japan) scanning electron microscope operated at 6–13 KV. Relative positions of radular teeth are shown in Figure 2c.

STATISTICAL METHODS

Statistical analyses were performed using the statistics packages "Statistix" Version 2 (NH Analytical Software) and "Systat" (Systat Incorporated).

Removal of Size Effects. — To eliminate the effect of size variation between specimens, enabling comparisons to be made between shape, for all statistical analyses of morphometric data residual variables were calculated following a method given by Winterbottom et al. (1984). The linear equation $Y = a + bML$ was used where: Y = the predicted value for an individual for any variable, a = intercept, b = slope, ML = mantle length. The residual variation represents a measure of the total deviation of the individual measurements from the regression line. A deviation from the line that describes the size relationship between the variables and standard length (ML) is given by $E = Y - \hat{Y}$. Thus E = the observed measure of shape (residual value) for any individual, Y is the observed value for the individual for a particular dependant variable and $\hat{Y}$ is the predicted value derived from the regression

Table 2. Enzymes examined, buffers used (Buf.) and tissue tested (Ts.) for each enzyme. Buffers: A = TC 100 pH 8.2, B = TEM 50 pH 7.8. E.C. No. = enzyme commission number, Abb. = abbreviation, DG = digestive gland, M = mantle, V = voltage

Enzyme	E.C. No.	Abb.	Ts.	Buf.	V
Aconitase	4.2.1.3	ACON	M	B	170
Acid phosphatase	3.1.3.2	ACP	DG	B	180
Alcohol dehydrogenase	1.1.1.1	ADH	DG	B	170
Adenylate kinase	2.7.4.3	AK	M	B	200
Aldolase	4.1.2.13	ALD	M	B	200
Aldehyde dehydrogenase	1.2.1.5	ALDH	DG	B	170
Esterase	3.1.1.1	EST	DG	B	180
Fructose-1,6-diphosphatase	3.1.3.11	FDP	M, DG	B	170
Fumarase	4.2.1.2	FUM	M	A	200
Glyceraldehyde 3-phosphate dehydrogenase	1.2.1.12	GAPD	M, DG	B	200
Aspartate amino transferase	2.6.1.1	GOT	DG, M	A	200
General protein		GP	M	B	170
αGlycerophosphate dehydrogenase	1.1.1.8	αGPD	M, DG	B	170
Glucose-6-phosphate dehydrogenase	1.1.1.49	G6PDH	DG	B	180
Glucose-phosphate isomerase	5.3.1.9	GPI	M, DG	B	170
Alanine amino transferase	2.6.1.2	GPT	DG	B	170
Hydroxybutyrate dehydrogenase	1.1.1.30	HBDH	DG	B	170
Hexokinase	2.7.1.1	HK	DG, M	B	180
Isocitrate dehydrogenase	1.1.1.42	IDH	M, DG	B	200
Lactate dehydrogenase	1.1.1.27	LDH	M	A	200
Malate dehydrogenase	1.1.1.37	MDH	M	B	200
Malic enzyme	1.1.1.40	ME	DG	B	180
Mannose-phosphate isomerase	5.3.1.8	MPI	M	B	170
6-Phosphogluconate dehydrogenase	1.1.1.44	6PGD	M, DG	B	170
Phosphoglycerate kinase	2.7.2.3	PGK	M	B	170
Phosphoglucomutase	2.7.5.1	PGM	M	B	200
Pyruvate kinase	2.7.1.40	PK	M	B	170
Triose-phosphate isomerase	5.3.1.1	TPI	M, DG	B	170
Xanthine oxidase	1.2.3.2	XO	DG	B	170

equation given above. Positive and negative residuals indicate larger and smaller than average body parts respectively. For each comparative analysis the regression was derived from the pooled set of data from all localities. Males and females were treated separately. When a locality group was excluded from any analysis, residuals were recalculated from new regression equations derived from remaining localities under consideration. Equations for the regression lines used to calculate residuals are given in Appendix 3.

Ratios (indices) were not used in the analyses as, according to Atchley et al. (1976), ratios should be avoided in morphometric studies because they can behave spuriously depending upon the correlation of the numerator and the denominator. In addition, the ratio is not necessarily independent of the denominator.

Principal Components Analysis (PCA). — In principal components analysis (PCA) new variables (components) are calculated that are linear combinations of the original variables such that the first component (PC1) explains most of the variance in the data. The second component is calculated so that it summarizes the next highest amount of variance in the data, subject to it being independent (aligned at right angles) to PC1. Subsequent components are calculated in a similar fashion. Most of the significant information is therefore contained within the first few components.

In this way, the net effects of a large number of characters may be examined without a need for a priori assignment of specimens to groups, thereby allowing for their discovery. Twenty-one morphometric characters were used in PCA and the first three principal components extracted based on a correlation matrix. These characters are indicated in Table 1. Plots of principal components scores, where not presented in results, are given in Appendix 4.

Multivariate Analysis of Variance (MANOVA). — Multivariate analysis of variance was used to determine whether a significant difference between localities was present based on all considered characters. The general validity of results based on principal components analysis, in which no a priori designation
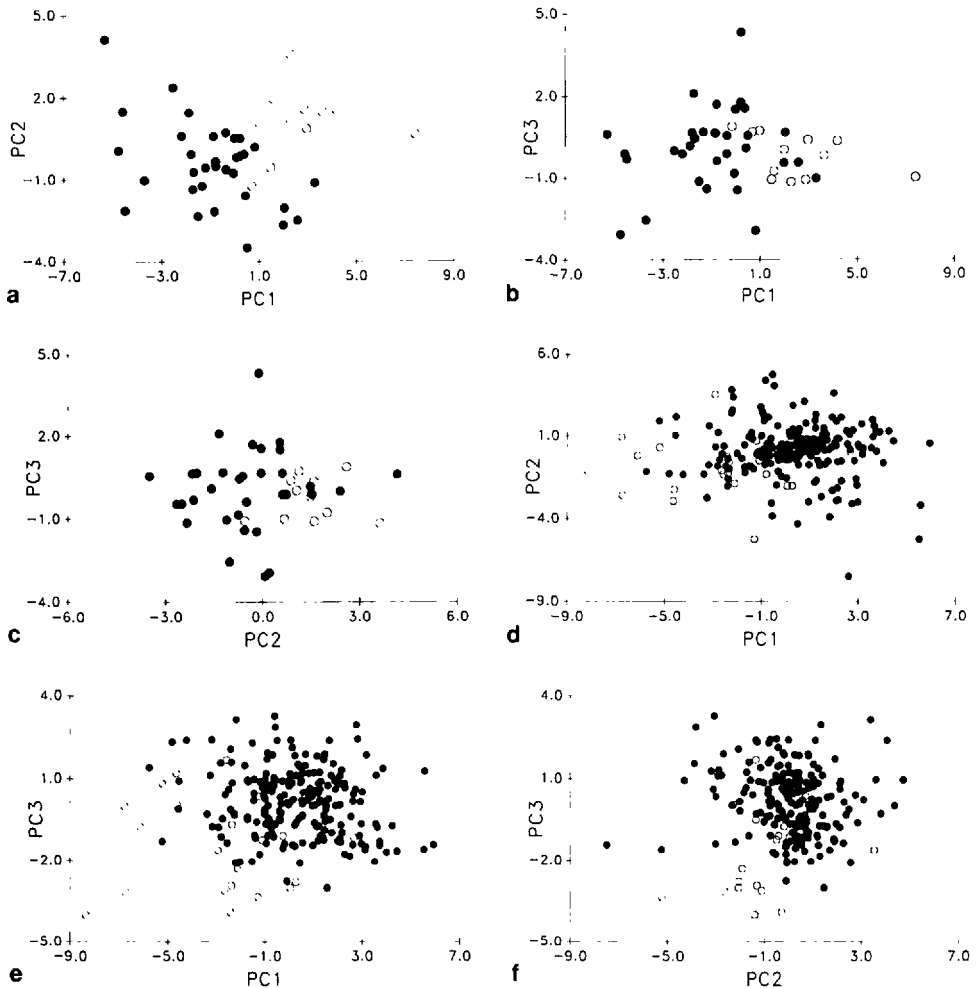
Figure 3. Scatter plots of first three PCA scores. a)–c) Australian *Rossia* males, d)–f) Australian *Rossia* females. a) and d) PC1 vs. PC2, b) and e) PC1 vs. PC3, c) and f) PC2 vs. PC3. Open circles = North West Shelf specimens, solid circles = eastern Australian specimens. Percent variance accounted for by the first three principal components for males: PC1 30.6%, PC2 13.0% and PC3 8.3% and females: PC1 25.0%, PC2 12.9% and PC3 8.7%.

of groups was required, was confirmed by MANOVA. The significance of MANOVA was tested using the Wilks' Lambda, Pillai Trace and Hotelling Lawley Trace F statistics. No difference in probabilities was found between any of these test statistics so MANOVA probabilities given in results refer to any test.

Discriminant Function Analysis (DFA) and Canonical Variates Analysis. —Once groupings suggested by PCA and confirmed by MANOVA were found, to further identify those characters which best differentiated the groups, DFA was performed using the same data sets described above. The pre-classified groups were tested to derive a function that discriminated the groups successfully. This function was then used in a predictive way to assign unknown specimens to the a priori groups.

The contribution of each character to the formation of the groups is contained in discriminant coefficients. Positive coefficients correspond to smaller than average body parts (negative residuals) and negative coefficients (positive residuals) to larger than average body parts.

Two females (AMS C161419) from Raine Island (Queensland) were initially excluded from the analysis. These specimens from this relatively isolated locality were treated later as unknowns.

In addition, by assigning specimens to selected groups based on locality, an extention of DFA,
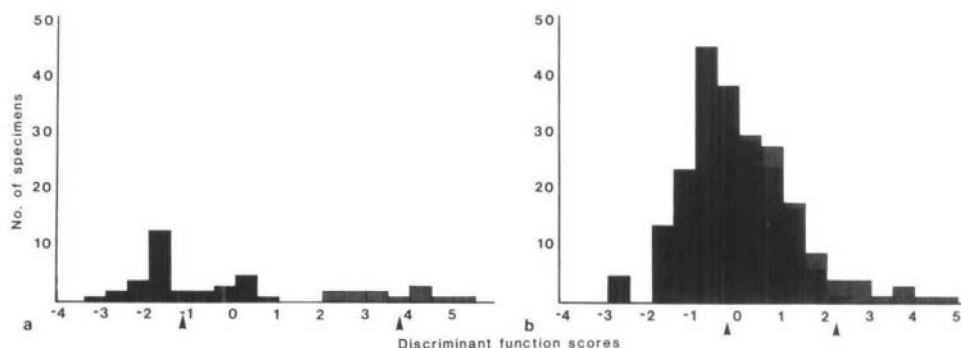
Figure 4.   Frequency histograms of residual scores on discriminant function between Group 1 (shaded bars) and Group 2 (solid bars) for Australian *Rossia* a) males and b) females. Arrows indicate group centroids.

canonical variates analysis, was used to examine aspects of geographic variation. Like DFA, canonical variates analysis applies the same strategy of optimizing distances between multivariate group means (centroids) but differs in that discrimination is between more than two groups.

Analysis of Variance (ANOVA).—Simple univariate analysis of variance was used to test the significance of mean differences in residual variables (reflecting differences in sizes of individual body parts) for groups identified by the above methods. ANOVA was also performed to detect differences in meristics. Variance between sample means was tested using an F test. The F test assumed that the within group variances are the same for each group. A Bartlett's test was used to examine equality of within group variances.

Latitudinal and Longitudinal Regression Analysis.—Regression of meristic variables and morphometric PCA scores and residuals against latitude and longitude of each specimen collection site was used to examine geographic variation. Distinct populations detected by the preceding techniques could reflect an ecophenotypic induction of differences or genotypic components (e.g., local selection for certain genotypes, partial restriction of gene flow, etc.). A continuous pattern of variation over the distributional range of specimens would suggest the presence of a single species. Discontinuity in the pattern of variation would suggest the presence of more than one.

For the southern hemisphere, when individual characters (residuals and meristics) are regressed against latitude, positive slopes for the regression lines will indicate that specimens from the southernmost latitudes have the greatest relative lengths or counts for the character tested (highest positive residuals), those from the northernmost latitudes will show the converse. If slopes are negative, the reverse relationship applies. Similarly, a positive slope when individual characters are regressed against longitude reflects greater relative lengths or counts for easternmost specimens for the character in question.

The null hypothesis in all analyses that tested hypotheses (i.e., MANOVA and regression vs. latitude and longitude) was that there was no difference in the values for a variable between groups or for latitude and longitude of sample collection site.

ELECTROPHORESIS

Digestive gland and mantle tissue dissected from each specimen was homogenized using the extracting buffer protocol of Richardson et al. (1986). Samples were run on cellulose acetate gels (Helena system) for 1 h at 170, 180 or 200 V. Individuals were screened for 28 enzymes and stained for nonenzymatic general proteins following methods of Richardson et al. (1986). Enzymes examined and running conditions for electrophoresis are given in Table 2.

RESULTS

Australian *Rossia*

MORPHOMETRIC ANALYSIS—RESIDUALS

Principal Components Analysis.—Equations for the regression lines used to calculate residuals for Australian *Rossia* are shown in Appendix 3a. When the scores

Table 3. Australian *Rossia* males. Means, analysis of variance significance (Sig.) and discriminant function coefficients for two group discriminant analysis for residuals from pooled regression lines. N = sample size, B.S. = Bartlett's test of significance for within-group variance, STD = standardized, UNSTD = unstandardized. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant

Variable	N	x̄ Grp. 1	x̄ Grp. 2	Sig.	B.S.	Coefficients STD	UNSTD
MW	45	−0.315	0.115	N/S	N/S	0.270	−0.033
HL	44	0.144	−0.054	N/S	N/S	0.085	0.018
HW	38	−0.197	0.907	**	N/S	—	—
ED	40	−1.204	0.516	N/S	N/S	—	—
NCL	44	−0.405	0.147	**	N/S	−0.349	−0.206
NCW	44	−0.185	0.069	**	N/S	−0.251	−0.204
FuL	44	0.669	−0.025	N/S	N/S	−0.055	0.085
AL I	37	−1.263	0.406	N/S	N/S	0.098	−0.075
AL II	37	−1.361	0.504	N/S	**	0.689	−0.073
AL III	40	−1.538	0.583	N/S	N/S	−0.080	−0.086
AL IV	38	−2.572	0.918	*	N/S	0.037	−0.170
ClL	23	7.878	−2.188	***	N/S	0.407	0.293
AS I	40	−0.208	0.095	***	N/S	0.242	−0.263
AS II	42	−0.438	0.175	***	N/S	−0.441	−0.540
AS III	43	−0.465	0.180	***	N/S	−0.846	−0.491
AS IV	41	−0.527	0.170	***	N/S	−0.405	−0.490
FP	43	0.416	−0.161	N/S	N/S	0.231	0.126
FI	45	0.292	−0.106	N/S	N/S	0.339	0.066
FL	45	−0.225	0.082	N/S	N/S	−0.253	−0.039
FWS	45	−0.074	0.027	N/S	N/S	0.351	−0.017
FWT	38	−0.700	0.285	N/S	N/S	0.283	−0.058

for principal components 1 (PC1) and 2 (PC2) calculated for males were plotted against each other, separation was noted between specimens from the North West Shelf and those from eastern and southeastern Australia (Fig. 3a). Considerable overlap between the groups was apparent when PC1 was plotted against PC3 and when PC2 was plotted against PC3 (Fig. 3b, c).

This group separation was not evident in females when PCA was performed. Almost complete overlap between the groups occurred in all three plots: PC1 vs. PC2, PC1 vs. PC3 and PC2 vs. PC3 (Fig. 3d–f).

When North West Shelf specimens were excluded, residuals recalculated (Appendix 3b) and PCA performed, no discrete clusters could be detected on any of the first three principal components for either males or females (Appendix 4-1 a–f).

Despite lack of separation seen in females in the first analysis with all specimens pooled, the clear separation of the North West Shelf and eastern Australian specimens in PC1 for males, with no a priori grouping assumption, suggests that two populations of Australian *Rossia* are present. Therefore, for subsequent analyses specimens were assigned to either Group 1 (North West Shelf) or Group 2 (eastern Australia).

Multivariate Analysis of Variance, Discriminant Function Analysis and Analysis of Variance.—Two characters for males (HW and ED), and six characters for females (ED, ClL, AS I, AS II, AS III and AS IV) were not included in the MANOVA or DFA based on latitudinal and longitudinal regression results (see below).

Multivariate analysis of variance calculated using the remaining morphometric

Table 4. Australian *Rossia* females. Means, analysis of variance significance (Sig.) and discriminant coefficients for two group discriminant function analysis for residuals from pooled regression lines. N = sample size, B.S. = Bartlett's test of significance for within-group variance, STD = standardized, UNSTD = unstandardized. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant

| | | | | | | Coefficients | |
Variable	N	x̄ Grp. 1	x̄ Grp. 2	Sig.	B.S.	STD	UNSTD
MW	224	2.513	−0.265	**	***	0.441	0.280
HL	220	2.875	−0.303	***	*	0.253	0.400
HW	204	−0.510	0.058	N/S	**	−0.524	−0.072
ED	218	−1.713	0.207	***	N/S	−	−
NCL	225	−0.554	0.068	*	N/S	−0.240	−0.209
NCW	223	−0.143	0.015	N/S	*	−0.196	−0.127
FuL	217	3.073	−0.314	***	*	0.487	0.691
AL I	187	4.917	−0.455	***	N/S	0.123	0.439
AL II	178	3.683	−0.331	***	N/S	0.036	0.327
AL III	188	3.359	−0.323	***	**	−0.009	0.303
AL IV	188	4.009	−0.372	***	**	0.078	0.372
ClL	137	12.040	−1.775	***	***	−	−
AS I	131	0.092	−0.009	*	N/S	−	−
AS II	127	0.016	−0.002	N/S	N/S	−	−
AS III	126	0.072	−0.007	N/S	N/S	−	−
AS IV	127	0.001	−0.0001	N/S	N/S	−	−
FP	214	1.705	−0.187	***	N/S	0.341	0.471
FI	222	1.232	−0.126	**	N/S	0.058	0.254
FL	217	1.447	−0.127	**	N/S	−0.009	0.227
FWS	218	1.543	−0.142	**	N/S	0.126	0.286
FWT	168	4.440	−0.505	***	N/S	0.070	0.361

characters showed a highly significant difference between the two populations for both males and females ($P \ll 0.0001$). As this test showed multivariate group centroids were significantly different, discriminant analyses were carried out.

No overlap between the two groups was seen in males with all specimens correctly classified (Fig. 4a). There was considerable overlap between the groups seen in females (Fig. 4b). Seventy-seven percent of specimens were correctly classified for Group 1 and 88% correctly classified for Group 2.

For males, mean residuals for Group 1 were negative for all characters with the exception of HL, FuL, ClL, FP and FI. Mean residuals for Group 2 were the reverse of the above. Nine variables showed significant univariate differences between the groups. For discriminant function results, the standardized function showed positive coefficients for MW, HL, AL I, AL II, AL IV, ClL, AS I, FP, FI, FWS and FWT, and negative coefficients for NCL, NCW, FuL, AL III, AS II, AS III, AS IV and FL (Table 3). Scores on the discriminant function were positive for specimens of Group 1 (centroid 3.604; range 2.145 to 5.314) and specimens of Group 2 generally had negative scores on the discriminant function (centroid −1.311; range −3.107 to 0.687).

For females, mean residuals for Group 1 were negative for HW, ED, NCL and NCW, the remaining characters showing positive values. Mean residuals for Group 2 were the reverse of the above. Sixteen characters showed significant univariate differences between the groups. It should be noted, however, that one of the assumptions for the F test, that of equality of group variance, was not met for eight characters (indicated by a significant Bartlett's test result). This is to be expected due to the large difference in sample size; Group 1, total N = 22, Group 2, total N = 205, a higher variance would undoubtedly be expected for Group 2.
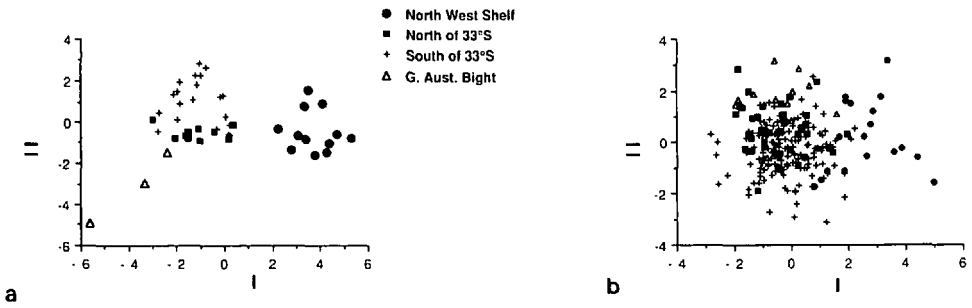
Figure 5. Scatter plots on the first two canonical axes of *Rossia* individuals divided into four groups by locality. a) males; b) females. Legend refers to both scatters.

Standardized functions resulting from a discriminant analysis showed positive coefficients for MW, HL, FuL, AL I, AL II, AL IV, FP, FI, FWS and FWT and negative coefficients for HW, NCL, NCW, AL III and FL (Table 4).

Group 1 specimens had positive scores on the discriminant function (centroid 2.302; range 0.338 to 4.774). Group 2 had negative and positive scores on the function centroid (centroid -0.261; range -2.969 to 2.381).

Rossia australis: The *R. australis* paratype (USNM 815719) clustered with Group 2 with a DFA score of -1.067. The probability that this specimen was correctly classified with this group was 0.995.

Raine Island Unknowns. —The two female specimens from Raine Island, not included in the construction of the discriminant function, were found also to

Table 5. Group 1 and Group 2 Australian *Rossia*. Means with significance (Sig.) for analysis of variance between groups for meristic variables. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant. N = sample size. B.S. = Bartlett's test of significance for within-group variance

| Variable	N	x̄ Group 1	x̄ Group 2	Sig.	B.S.
a. Males					
CIRC	22	24.20	21.71	N/S	N/S
ASC I	41	20.33	21.69	N/S	N/S
ASC II	43	15.91	17.12	N/S	N/S
ASC III	41	15.90	17.29	N/S	N/S
ASC IV	44	17.27	17.94	N/S	N/S
ASCT I	20	52.27	58.56	N/S	*
ASCT II	20	47.60	58.00	*	*
ASCT III	20	48.73	52.55	N/S	***
ASCT IV	22	56.09	62.64	N/S	N/S
GiLC	26	23.29	22.95	N/S	*
b. Females				'	
CIRC	112	36.92	30.09	***	**
ASC I	210	20.58	21.29	N/S	N/S
ASC II	201	20.18	21.07	*	N/S
ASC III	207	20.35	20.62	N/S	*
ASC IV	211	20.65	21.50	N/S	N/S
ASCT I	53	63.40	72.61	**	N/S
ASCT II	55	64.40	74.82	***	N/S
ASCT III	50	67.73	74.46	**	N/S
ASCT IV	55	74.00	83.10	**	N/S
GiLC	104	25.20	24.83	N/S	***
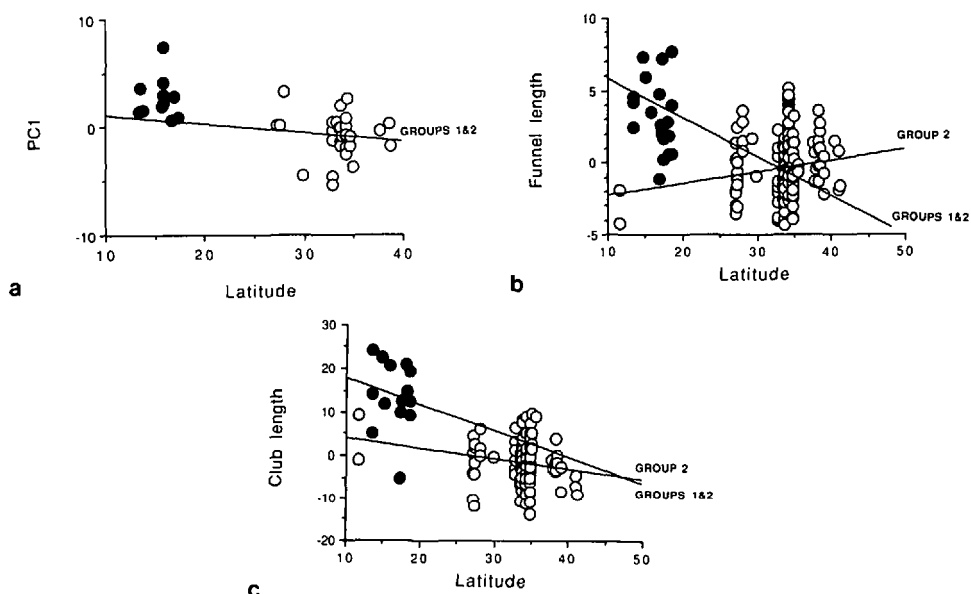
Figure 6. a) Regression of PC1 against latitude, *Rossia* males, Groups 1 and 2. b) Regression of FuL against latitude, *Rossia* females Groups 1 and 2. c) Regression of ClL against latitude, *Rossia* females Groups 1 and 2. Closed circles = Group 1 specimens, open circles = Group 2.

cluster with Group 2 when treated as unknowns in a repeated analysis. Discriminant function scores were −1.254 and −1.754. The strength of this classification was indicated by high probability scores of 0.997 and 0.999.

Canonical Variates Analysis.—In addition to latitudinal and longitudinal regression analyses discussed below, a canonical variates analysis was used to look for

Table 6. Australian *Rossia* Groups 1 and 2 (a, b) and Group 2 (c, d). Regression of first three principal components against latitude and longitude tested by $Y = a + bX$ where Y = the predicted dependent variable, a = y intercept, b = slope, X is either latitude or longitude. Significance level of association (Sig.), *** $P < 0.001$, N/S = not significant. r^2 = proportion of total variation accounted for by regression

Variable		$X =$ Latitude				$X =$ Longitude		
	Sig.	r^2	a	b	Sig.	r^2	a	b
a. Males								
PC1	***	0.365	5.23	−0.177	***	0.340	14.67	−0.102
PC2	***	0.193	2.51	−0.088	***	0.215	7.87	−0.055
PC3	N/S	0.009	−0.34	0.015	N/S	0.011	−1.25	0.009
b. Females								
PC1	***	0.093	−3.65	0.113	***	0.091	−10.53	0.071
PC2	N/S	0.001	−0.17	0.007	***	0.111	−8.11	0.055
PC3	***	0.121	−2.51	0.078	***	0.108	−6.92	0.047
c. Males								
PC1	N/S	0.005	2.43	−0.066	N/S	0.003	7.22	−0.046
PC2	N/S	0.001	−0.66	0.019	N/S	0.031	−16.08	0.106
PC3	N/S	0.022	2.76	−0.079	N/S	0.001	−1.92	0.013
d. Females								
PC1	N/S	0.000	−0.03	−0.003	***	0.040	19.61	−0.130
PC2	***	0.094	4.55	−0.134	***	0.155	−28.15	0.187
PC3	N/S	0.010	1.17	−0.035	N/S	0.011	6.04	−0.040

Table 7. Australian *Rossia* Groups 1 and 2 males. Latitudinal and longitudinal regression of variables tested by $Y = a + bX$ where Y = the predicted dependent variable, a = y intercept, b = slope, X is either latitude or longitude. Significance level of association (Sig.), *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant. r^2 = proportion of total variation accounted for by regression

Variable	X = Latitude				X = Longitude			
	Sig.	r^2	a	b	Sig.	r^2	a	b
Residuals								
MW	N/S	0.008	−0.81	0.028	N/S	0.004	−1.81	0.013
HL	N/S	0.001	0.38	−0.009	N/S	0.0001	−0.27	0.003
HW	***	0.301	−5.09	0.186	***	0.196	−12.51	0.089
ED	***	0.200	−3.67	0.135	*	0.093	−7.72	0.055
NCL	**	0.157	−0.83	0.029	**	0.139	−2.29	0.016
NCW	**	0.151	−0.37	0.013	**	0.167	−1.14	0.008
FuL	N/S	0.014	0.89	−0.031	N/S	0.042	4.64	−0.032
AL I	N/S	0.021	−2.29	0.068	N/S	0.030	−6.97	0.047
AL II	N/S	0.016	−2.28	−0.069	N/S	0.030	−8.12	0.055
AL III	N/S	0.041	−3.27	0.095	N/S	0.018	−0.61	0.038
AL IV	**	0.139	−5.21	0.173	**	0.142	−15.60	−0.107
CIL	***	0.690	16.57	−0.564	***	0.610	44.36	−0.307
AS I	***	0.251	−0.47	0.016	***	0.246	−1.37	0.009
AS II	***	0.620	−0.92	0.032	***	0.592	−2.64	0.018
AS III	***	0.536	−0.96	0.033	***	0.546	−2.85	0.020
AS IV	***	0.624	−1.03	0.035	***	0.628	−3.09	0.021
FP	N/S	0.041	0.64	−0.023	*	0.087	2.78	−0.019
FI	N/S	0.012	0.47	−0.016	N/S	0.032	2.20	−0.015
FL	N/S	0.004	−0.38	0.012	N/S	0.004	−1.09	0.007
FWS	N/S	0.0002	−0.09	0.002	N/S	0.0001	0.08	−0.001
FWT	N/S	0.020	−1.53	0.055	N/S	0.021	−4.82	0.034
Meristics								
CIRC	*	0.220	26.92	−0.160	*	0.186	34.44	0.084
ASC I	N/S	0.073	19.08	0.077	N/S	0.013	16.45	0.034
ASC II	**	0.123	14.49	0.080	N/S	0.046	12.72	0.028
ASC III	*	0.082	14.58	0.077	N/S	0.026	13.07	0.026
ASC IV	N/S	0.065	16.05	0.062	N/S	0.009	15.80	0.015
ASCT I	N/S	0.070	48.60	0.267	N/S	0.139	19.10	0.269
ASCT II	N/S	0.154	41.87	0.431	**	0.323	−5.58	0.431
ASCT III	N/S	0.019	47.52	0.124	N/S	0.105	23.36	0.202
ASCT IV	N/S	0.079	52.64	0.267	*	0.179	21.58	0.279
GiLC	N/S	0.022	23.78	−0.028	N/S	0.011	24.71	−0.012

evidence of clinal trends. The analysis was performed using all specimens and further dividing Group 2 into three subgroups by locality; North of 33°S (2a), South of 33°S (2b) and (2c), Great Australian Bight (west of approximately 146°E).

For males, all specimens were correctly classified for Groups 1 and 2c, 90% of specimens were correctly classified for Group 2a and 95% correctly classified for Group 2b. Figure 5a shows three clusters detected when individuals are plotted on the first two canonical axes.

In females, there is considerable overlap between clusters (Fig. 5b) with some separation seen between Group 1 and the eastern Australian groups. Seventy-seven percent of specimens were correctly classified for Group 1, 50% for Group 2a, 54% for Group 2b and 61% of specimens were correctly classified for Group 2c.

MERISTIC ANALYSIS

Ten meristic variables were examined. These data were subjected to ANOVA only: many of these characters were expected a priori to correlate highly with

Table 8. Australian *Rossia* Groups 1 and 2 females. Latitudinal and longitudinal regression of variables tested by $Y = a + bX$ where Y = the predicted dependent variable, a = y intercept, b = slope, X is either latitude or longitude. Significance level of association (Sig.), *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant. r^2 = proportion of total variation accounted for by regression

Variable	X = Latitude				X = Longitude			
	Sig.	r^2	a	b	Sig.	r^2	a	b
Residuals								
MW	N/S	0.011	2.12	−0.069	**	0.026	9.60	−0.065
HL	***	0.070	4.63	−0.145	***	0.053	11.69	−0.079
HW	*	0.016	−2.04	0.064	N/S	0.009	−4.42	0.029
ED	***	0.068	−2.79	0.089	***	0.116	−10.92	0.074
NCL	*	0.019	−0.85	0.027	**	0.022	−2.74	0.018
NCW	N/S	0.009	−0.24	0.008	N/S	0.010	−0.77	0.005
FuL	***	0.105	3.74	−0.117	***	0.207	15.25	−0.103
AL I	***	0.056	5.74	−0.176	***	0.058	17.08	−0.115
AL II	*	0.025	3.57	−0.111	***	0.052	15.93	−0.108
AL III	N/S	0.015	2.86	−0.090	**	0.028	11.63	−0.079
AL IV	***	0.046	4.91	−1.506	***	0.042	13.66	−0.092
CIL	***	0.400	21.57	−0.678	***	0.420	66.51	−0.450
AS I	***	0.136	0.36	−0.011	N/S	0.0001	−0.02	0.000
AS II	**	0.050	0.25	−0.007	*	0.032	−0.53	0.004
AS III	***	0.061	0.28	−0.008	N/S	0.000	−0.02	0.000
AS IV	N/S	0.010	0.08	−0.002	*	0.028	−0.34	0.002
FP	***	0.063	2.25	−0.070	***	0.093	7.84	−0.053
FI	*	0.018	1.51	−0.047	***	0.038	6.32	−0.043
FL	N/S	0.006	1.14	−0.035	***	0.033	7.55	−0.051
FWS	**	0.028	2.09	−0.065	***	0.033	6.52	−0.044
FWT	N/S	0.010	3.30	−0.106	***	0.073	20.66	−0.141
Meristics								
CIRC	***	0.383	40.97	−0.320	***	0.359	60.33	−0.200
ASC I	N/S	0.013	20.06	0.037	N/S	0.009	18.44	0.019
ASC II	**	0.025	19.47	0.046	N/S	0.000	20.88	0.001
ASC III	N/S	0.001	20.81	−0.007	N/S	0.013	23.67	−0.020
ASC IV	***	0.045	19.17	0.070	N/S	0.002	20.03	0.009
ASCT I	**	0.108	59.55	0.375	***	0.210	25.63	0.321
ASCT II	**	0.128	60.80	0.397	***	0.296	20.46	0.361
ASCT III	**	0.110	63.73	0.313	***	0.203	36.19	0.255
ASCT IV	**	0.111	68.32	0.435	***	0.162	35.84	0.313
GiLC	N/S	0.014	25.87	−0.029	N/S	0.008	22.73	0.014

each other (e.g., ASC and ASCT) while others had many missing values (e.g., GiLC) and were therefore not appropriate for multivariate analyses. No difference between the two groups for nine characters was detected for males. However, a significant difference occurred between counts for ASCT II, with specimens from Group 2 having a greater number of suckers than in Group 1, but within group variance differences as indicated by a Bartlett's test was high (Table 5a). In females, CIRC and ASC II differed significantly between the two groups, with mean CIRC Group 1 greater than for Group 2. ASC II was very slightly but significantly greater in Group 2 than Group 1. Again, however, a significant Bartlett's test result for CIRC suggests high difference between within group variances. Total arm sucker counts for all arms differed significantly between the groups with Group 2 having a greater number of arm suckers in each case (Table 5b).

LATITUDINAL AND LONGITUDINAL REGRESSION ANALYSES

With three exceptions (PC3 with latitude and longitude in males and PC2 with latitude in females), each of the first three principal components for males and

Table 9. Australian *Rossia* Group 2 males. Latitudinal and longitudinal regression of variables tested by $Y = a + bX$ where Y = the predicted dependent variable, a = y intercept, b = slope, X is either latitude or longitude. Significance level of association (Sig.), *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant. r^2 = proportion of total variation accounted for by regression

Variable	X = Latitude				X = Longitude			
	Sig.	r^2	a	b	Sig.	r^2	a	b
Residuals								
MW	N/S	0.0001	0.40	−0.012	N/S	0.001	−4.61	0.030
HL	N/S	0.051	6.73	−0.197	N/S	0.064	−30.70	0.204
HW	*	0.148	−13.06	0.393	N/S	0.079	37.76	−0.249
ED	***	0.316	−18.33	0.549	N/S	0.098	42.30	−0.279
NCL	N/S	0.016	0.81	−0.024	N/S	0.002	5.05	−0.033
NCW	N/S	0.006	0.27	0.008	N/S	0.031	−2.57	0.017
FuL	N/S	0.076	−8.28	0.246	N/S	0.014	14.57	−0.096
AL I	N/S	0.004	2.92	−0.097	N/S	0.036	−36.30	0.238
AL II	N/S	0.006	4.91	−0.157	N/S	0.028	−42.88	0.281
AL III	N/S	0.053	−12.63	0.352	N/S	0.019	28.45	−0.193
AL IV	N/S	0.014	−6.13	0.174	N/S	0.004	−13.78	0.089
ClL	N/S	0.113	14.21	−0.431	N/S	0.154	−67.48	0.444
AS I	N/S	0.007	−0.35	0.010	N/S	0.0004	0.40	−0.003
AS II	N/S	0.029	−0.50	0.014	N/S	0.001	−0.34	0.002
AS III	N/S	0.009	−0.35	0.009	N/S	0.001	−0.52	0.003
AS IV	N/S	0.010	−0.32	0.009	N/S	0.0001	0.08	−0.001
FP	N/S	0.084	−3.81	0.114	N/S	0.0002	9.88	−0.006
FI	N/S	0.0007	−0.40	0.012	N/S	0.019	9.21	−0.061
FL	N/S	0.002	1.00	−0.031	N/S	0.0001	0.77	−0.005
FWS	N/S	0.0001	−0.21	0.004	N/S	0.056	15.19	−0.101
FWT	N/S	0.0000	0.16	−0.004	N/S	0.0003	2.86	−0.019
Meristics								
CIRC	N/S	0.082	31.90	−0.307	N/S	0.055	55.16	−0.221
ASC I	N/S	0.012	17.72	0.116	N/S	0.098	62.22	−0.268
ASC II	*	0.107	9.12	0.238	**	0.197	62.49	−0.300
ASC III	N/S	0.042	10.17	0.026	***	0.263	80.11	−0.417
ASC IV	N/S	0.090	9.60	−0.254	***	0.238	76.27	−0.384
ASCT I	N/S	0.124	122.76	−1.82	N/S	0.317	−227.04	1.910
ASCT II	N/S	0.308	159.73	−2.89	**	0.573	−330.05	2.590
ASCT III	N/S	0.228	140.34	−2.50	**	0.521	−321.06	2.490
ASCT IV	N/S	0.167	128.08	−1.87	*	0.413	−227.62	1.940
GiLC	N/S	0.024	27.00	−0.123	N/S	0.013	13.50	0.062

females were significantly correlated with both latitude and longitude when Groups 1 and 2 were included (Table 6a, b). When PC scores from the analysis excluding Group 1 were regressed against latitude and longitude, no correlation in any of the first three components between latitude and longitude was detected in males (Table 6c, Fig. 6a). In females, PC1 correlated with longitude and PC2 correlated with latitude and longitude (Table 6d).

When each variable was examined separately, in males with both groups included, three meristic and 10 morphometric variables correlated significantly with latitude, while three meristic and 11 morphometric characters correlated significantly with longitude (Table 7).

In females, seven meristic and 15 morphometric variables correlated significantly with latitude. Five meristic and 17 morphometric variables correlated significantly with longitude (Table 8).

When Group 1 specimens were excluded and residuals and regressions recalculated for males, one meristic and two morphometric characters correlated sig-

Table 10. Australian *Rossia* Group 2 females. Latitudinal and longitudinal regression of variables tested by $Y = a + bX$ where $Y =$ the predicted dependent variable, $a =$ y intercept, $b =$ slope, X is either latitude or longitude. Significance level of association (Sig.), *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant

Variable	X = Latitude				X = Longitude			
	Sig.	r^2	a	b	Sig.	r^2	a	b
Residuals								
MW	N/S	0.003	−1.74	0.051	N/S	0.007	13.29	−0.088
HL	N/S	0.004	1.71	−0.051	N/S	0.006	−10.74	0.071
HW	N/S	0.009	−2.50	0.076	N/S	0.004	8.10	−0.054
ED	N/S	0.005	−1.16	0.037	***	0.070	−23.63	0.157
NCL	N/S	0.0004	−0.21	0.006	N/S	0.0001	−0.42	0.003
NCW	N/S	0.0000	0.02	−0.0003	N/S	0.0003	−0.35	0.002
FuL	*	0.017	−2.23	0.066	N/S	0.0002	1.25	−0.008
AL I	N/S	0.003	−1.96	0.063	***	0.073	−48.24	0.320
AL II	N/S	0.011	−3.88	0.115	N/S	0.010	−22.01	0.145
AL III	N/S	0.014	−4.34	0.131	**	0.030	−32.61	0.216
AL IV	N/S	0.001	−1.15	0.037	**	0.033	−29.92	0.198
CIL	***	0.086	11.27	−0.335	N/S	0.0003	−3.97	0.026
AS I	***	0.190	0.78	−0.023	***	0.213	−2.92	0.019
AS II	***	0.238	1.10	−0.032	***	0.214	−3.55	0.024
AS III	***	0.095	0.65	−0.019	***	0.102	−2.43	0.016
AS IV	***	0.112	0.47	−0.014	***	0.112	−1.66	0.011
FP	N/S	0.0007	−0.38	0.012	N/S	0.003	−3.74	0.025
FI	N/S	0.0002	−0.21	0.007	N/S	0.005	6.24	−0.041
FL	N/S	0.008	−2.18	0.026	N/S	0.003	6.74	−0.044
FWS	N/S	0.0001	0.17	−0.005	N/S	0.006	−7.93	0.052
FWT	*	0.032	−8.17	0.242	N/S	0.008	17.42	−0.116
Meristics								
CIRC	***	0.071	35.18	−0.150	N/S	0.003	36.89	−0.045
ASC I	N/S	0.0002	21.08	0.007	N/S	0.003	25.50	−0.028
ASC II	*	0.018	18.92	0.062	***	0.061	40.45	−0.128
ASC III	N/S	0.0004	20.27	0.009	***	0.081	41.64	−0.139
ASC IV	***	0.036	18.07	0.101	***	0.045	39.40	−0.119
ASCT I	N/S	0.008	77.30	−0.146	N/S	0.031	13.98	0.389
ASCT II	N/S	0.034	83.65	−0.274	N/S	0.055	4.21	0.469
ASCT III	N/S	0.0001	74.94	−0.015	*	0.096	−7.65	0.546
ASCT IV	N/S	0.0001	83.67	−0.018	N/S	0.015	36.73	0.308
GiLC	***	0.071	35.18	−0.153	***	0.084	13.15	0.078

nificantly with latitude. Six meristic characters correlated significantly with longitude. No morphometric characters correlated with longitude (Table 9).

In females, with exclusion of Group 1, four meristic and seven morphometric variables correlated significantly with latitude. Five meristic characters and eight morphometric variables covaried significantly with longitude (Table 10).

Additional supportive evidence for the validity of the existence of two groups can be seen in Figure 6b which shows regression of FuL against latitude for females. In this case, although correlation is significant when both groups are included and when Group 1 is excluded, the slopes of the regressions have opposite signs. This indicates that the Group 1 specimens are pulling the regression in the opposite direction when both groups are included.

This same relationship of slope reversal after the removal of Group 1 specimens was detected also for AL I, AL III and AL IV in females with respect to longitude (Tables 8, 10).

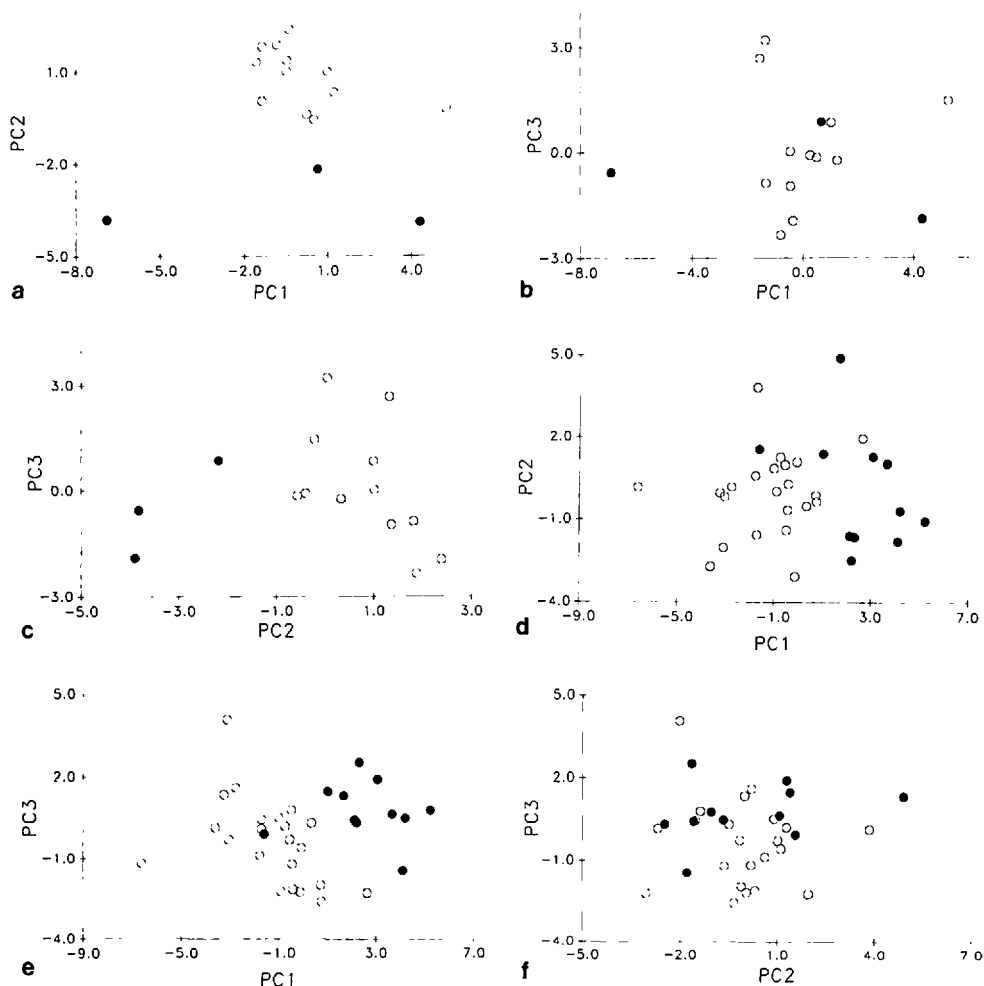It should also be noted that this relationship for these characters, which were

Figure 7. Scatter plots of the first three PCA scores. a)–c) Group 1 and *Rossia mastigophora* males, d)–f) Group 1, and *R. mastigophora* females. a) and d) PC1 vs. PC2, b) and e) PC1 vs. PC3, c) and e) PC2 vs. PC3. Open circles = Group 1, solid circles = *R. mastigophora*. Percent variance acounted for by the first three principal components for males: PC1 35.5%, PC2 18.1% and PC3 12.3% and females: PC1 32.7%, PC2 14.5% and PC3 10.9%.

included in DFA, lowers the discriminating power of DFA. This is because although the characters are clearly informative in distinguishing the two populations, values for Group 2 specimens from the southernmost localities may overlap those for Group 1 specimens. This can be seen in Figure 6b for FuL.

Exclusion of Characters from Multivariate Analysis of Variance and Discriminant Function Analysis. — As mentioned above, two characters for males (HW and ED) and six characters for females (ED, CIL, AS I, AS II, AS III and AS IV) were not included in the MANOVA or the DFA. Significant latitudinal correlation was noted in males for HW and ED and in females for CIL, AS I, AS II and AS III. ED, AS II and AS IV correlated significantly with longitude in females. In each case the slopes of the regression lines for each of the characters were of the same sign with Groups 1 and 2 pooled and with Group 1 excluded.
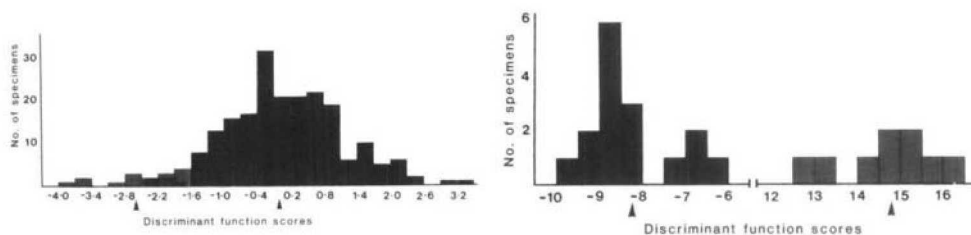
Figure 8. Frequency histogram of residual scores on discriminant function between Group 2 Australian *Rossia* females (solid bars) and *Rossia mastigophora* females (shaded bars). Arrows indicate group centroids.

Figure 9 (right). Frequency histogram of residual scores on discriminant function between Australian *Neorossia* (solid bars) and *Neorossia caroli* females (shaded bars). Arrows indicate group centroids.

An example is given in Figure 6c, which shows regression of ClL against latitude for females. Significant regression results (with negative slopes), both with Groups 1 and 2 included, and with Group 1 excluded, suggest club length decreases with increasing latitude.

Significant correlations with latitude or longitude may represent ecophenotypic responses to some covarying environmental factor. Since Groups 1 and 2 are spatially isolated from each other, any observed differences between the two groups for the above characters may simply represent ecophenotypic variation. It was, therefore, necessary to exclude these characters from the MANOVAs and DFAs.

Comparison with African *Rossia* Species

As no individual quantitative or qualitative characters were found to distinguish Australian *Rossia* from the African *Rossia* specimens available for study, a statistical approach was again applied.

MORPHOMETRIC ANALYSIS

Principal Components Analysis. — Data on each species were subjected to PCA using methods as previously described. Appendix 3c gives regression equations used to calculate residuals for Group 1 and *R. mastigophora* males and females. Complete separation in PC2 was detected for males (Fig. 7a, c). There was no separation in either PC1 (Fig. 7a, b) or PC3 (Fig. 7b, c).

In females, separation was noted in PC1 when plotted against PC2 and PC3 (Fig. 7d, e). No separation was detected when PC2 was plotted against PC3 (Fig. 7f).

Comparison of Group 2 with the same African specimens yielded a contrasting result. Equations for regression lines used to calculate residuals are given in Appendix 3d. No separation between Group 2 and the two African species on any of the first three components was apparent for either sex (Appendix 4-2).

Multivariate Analysis of Variance, Discriminant Function Analysis and Analysis of Variance. — Although PCA did not discriminate between Group 2 and *R. mastigophora,* as the sample represented two geographically isolated populations, the data was further subjected to MANOVA. Males were not analyzed as only three *R. mastigophora* specimens were available. Using the a priori designated groups, MANOVA results indicated that multivariate centroids were significantly different for females $P < 0.0001$ enabling DFA to be performed.

Table 11. *Rossia* (Group 2) and *R. mastigophora* (Group 3) females. Means, analysis of variance significance (Sig.) and discriminant function coefficients for two group discriminant analysis for residuals from pooled regression lines. N = sample size, B.S. = Bartlett's test of significance for within-group variance, STD = standardized, UNSTD = unstandardized. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant

Variable	N	x̄ Grp. 2	x̄ Grp. 3	Sig.	B.S.	Coefficients STD	UNSTD
MW	215	0.081	−1.507	N/S	N/S	0.378	0.159
HL	211	0.125	−2.279	**	*	0.241	0.291
HW	196	0.144	−2.420	**	N/S	0.367	0.325
ED	209	0.094	−1.689	**	N/S	0.279	0.320
NCL	216	0.004	−0.079	N/S	*	0.036	0.025
NCW	215	−0.018	0.327	*	N/S	−0.243	−0.251
FuL	209	−0.009	0.164	N/S	N/S	−0.112	−0.034
AL I	180	0.090	−1.710	N/S	*	−0.010	0.138
AL II	171	0.128	−2.602	N/S	N/S	0.195	0.190
AL III	181	0.018	−0.309	N/S	N/S	−0.267	0.027
AL IV	181	0.156	−2.975	*	N/S	0.262	0.257
CIL	133	0.233	−2.587	N/S	N/S	0.071	0.254
AS I	130	−0.0002	0.003	N/S	N/S	−0.561	−0.008
AS II	124	0.003	−0.036	N/S	N/S	−0.102	0.079
AS III	124	0.001	−0.012	N/S	N/S	−0.020	0.028
AS IV	124	0.009	−0.127	N/S	N/S	0.638	0.372
FP	206	−0.005	8.227	N/S	N/S	0.067	−0.020
FI	213	−0.098	1.810	**	N/S	−0.427	−0.331
FL	209	−0.106	1.911	*	N/S	−0.211	−0.271
FWS	210	−0.024	0.441	N/S	N/S	0.102	−0.075
FWT	161	−0.125	1.885	N/S	N/S	−0.382	−0.156

Overlap between the two groups was slight with all *R. mastigophora* specimens correctly classified and 93% of Group 2 specimens classified correctly (Fig. 8).

Mean residuals for Group 2 were negative for NCW, FuL, AS I, FP, FI, FL, FWS and FWT. The remaining characters showed positive scores. *R. mastigophora* specimens (labelled Group 3 in tables) show the reverse pattern. Seven characters showed significant univariate differences between the groups. For discriminant function results, the standardized function showed positive coefficients for MW, HL, HW, ED, NCL, AL II, AL IV, CIL, AS IV, FP and FWS and negative coefficients for the remaining variables (Table 11). Scores on the discriminant

Table 12. *Rossia* (Group 2) and *R. mastigophora* (Group 3) females. Means and significance (Sig.) for analysis of variance between groups for meristic variables. B.S. = Bartlett's test of significance for within-group variance. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant

Variable	N	x̄ Group 2	x̄ Group 3	Sig.	B.S.
CIRC	112	30.12	26.55	***	***
ASC I	204	21.30	20.55	N/S	N/S
ASC II	196	21.06	20.80	N/S	N/S
ASC III	200	20.62	20.73	N/S	N/S
ASC IV	204	21.50	21.27	N/S	N/S
ASCT I	52	72.61	66.86	*	N/S
ASCT II	51	74.82	68.55	*	N/S
ASCT III	47	74.46	78.25	N/S	N/S
ASCT IV	53	83.10	75.15	*	*
GiLC	110	24.85	24.90	N/S	N/S

Table 13. Australian *Neorossia* (Group 1) and *N. caroli* (Group 2) females. Means, analysis of variance significance (Sig.) and discriminant function analysis for residuals from pooled regression lines. N = sample size, B.S. = Bartlett's test of significance for within-group variance, STD = standardized, UNSTD = unstandardized. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant

Variable	N	x̄ Grp. 1	x̄ Grp. 2	Sig.	B.S.	Coefficients	
						STD	UNSTD
MW	25	1.964	−3.492	***	N/S	−72.339	−0.007
HL	25	0.733	−1.303	N/S	N/S	25.133	0.029
HW	25	1.100	−1.955	N/S	N/S	−2.570	−0.027
ED	25	0.092	−0.164	N/S	N/S	29.253	−0.004
NCL	25	0.038	−0.068	N/S	N/S	−6.108	−0.005
NCW	25	0.410	−0.729	***	N/S	8.830	−0.070
FuL	25	−0.254	0.452	N/S	N/S	−12.974	0.010
AL I	24	0.981	−1.636	N/S	*	5.051	−0.022
AL II	25	−0.370	0.658	N/S	N/S	−38.022	0.010
AL III	25	−0.724	1.287	N/S	N/S	13.853	0.017
AL IV	25	−0.169	0.337	N/S	N/S	−1.216	0.004
CIL	24	0.968	−1.613	N/S	N/S	8.535	−0.022
AS I	25	0.068	−0.120	N/S	N/S	48.998	−0.035
AS II	25	0.112	−0.198	**	N/S	−4.235	−0.056
AS III	25	0.086	−0.153	*	N/S	−51.078	−0.038
AS IV	25	0.038	−0.068	N/S	N/S	29.926	−0.018
FP	25	0.064	−0.115	N/S	N/S	28.014	0.00
FI	25	0.051	−0.905	N/S	N/S	12.627	−0.020
FL	25	0.210	−0.373	N/S	N/S	−19.654	−0.006
FWS	24	0.590	−1.179	N/S	N/S	24.084	−0.020
FWT	24	2.709	−5.418	*	N/S	28.996	−0.043

function were negative for *R. mastigophora* (centroid −2.68; range −3.86 to −1.70) and specimens from Group 2 had both negative and positive scores on the discriminant function though the centroid was positive (0.14; range −2.45 to 3.27).

Meristic Analysis. —As the sample size was so small for *R. mastigophora* males, again only females were subjected to statistical analyses. CIRC, ASCT I, ASCT II and ASCT IV showed significant univariate difference between means with Group 2, showing greater number of club and arm suckers in each case than *R. mastigophora*. Within group variance was high as indicated by Bartlett's test for CIRC and ASCT IV (Table 12).

NEOROSSIA: Qualitative Characters. —A difference in radula structure was noted between *N. caroli* and specimens of *Neorossia* from Australia. The rhachidian and first lateral teeth of *N. caroli* are broad and leaf-shaped, with indented bases, while those of similar-sized Australian *Neorossia* are relatively narrow and more triangular, with truncate bases. These differences are apparent in specimens across a size range and were noted in both sexes (Figs. 25d–f and 30c–f).

MORPHOMETRIC ANALYSIS

Principal Components Analysis. —Regression lines used to calculate residuals for Australian *Neorossia* and *N. caroli* are shown in Appendix 3e. Considerable overlap resulted between these two populations for both males and females when the first three principal component scores were plotted against each other (Appendix 4-3).

Table 14. Australian *Neorossia* (Group 1) and *N. caroli* (Group 2) females. Means and significance (Sig.) for analysis of variance between groups for meristic variables. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant. B.S. = Bartlett's test of significance for within-group variance

Variable	N	x̄ Group 1	x̄ Group 2	Sig.	B.S.
CIRC	24	9.93	9.67	N/S	***
ASC I	25	20.19	19.56	N/S	N/S
ASC II	25	19.31	21.33	*	N/S
ASC III	25	21.19	23.33	*	N/S
ASC IV	25	21.81	23.00	N/S	N/S
ASCT I	25	51.62	56.33	N/S	N/S
ASCT II	25	57.12	62.33	N/S	N/S
ASCT III	25	59.81	69.67	***	N/S
ASCT IV	25	61.62	69.56	**	*
GiLC	22	19.60	20.14	N/S	**

Multivariate Analysis of Variance, Discriminant Function Analysis and Analysis of Variance. — As these specimens were obtained from quite different geographic localities and since a qualitative character difference was found, further examination using MANOVA was justified despite the fact that PCA did not discriminate groups. As only three males of Australian *Neorossia* were available at the time of writing, only females were analyzed. MANOVA results showed a significant difference between the two populations of *Neorossia* females ($P < 0.05$). As this test shows group centroids were different, a DFA was performed.

No overlap between the two groups was seen in females and a posteriori accuracy was high with all specimens correctly classified (Fig. 9).

Mean residuals for Australian *Neorossia* (Group 1) were positive for all characters with the exception of FuL, AL II, AL III and AL IV (Table 13). *Neorossia caroli* (Group 2) showed the reverse of the above. Only five variables showed significant univariate differences between means: MW, NCW, AS II, AS III and FWT.

For discriminant function results, the standardized function showed positive coefficients for all characters with the exception of MW, HW, NCL, FuL, AL II, AL IV, AS II, AS III and FL. Specimens of the Australian *Neorossia* had negative scores on the discriminant function (centroid -8.21, range 9.62 to -6.44) and *Neorossia caroli* had positive scores on the discriminant function (centroid 14.72, range 12.87 to 16.31).

Meristic Analysis. — For meristic variables, ASC II, ASC III, ASCT III and ASCT IV showed significant univariate differences between means (Table 14), with *Neorossia caroli* showing higher counts than Australian *Neorossia* for each variable.

Electrophoresis

Activity was detected for 19 of the 28 enzymes screened. These were: ACP, ADH, ALD, EST, FDP, FUM, GAPD, αGPD, GPI, GPT, IDH, MDH, ME, MPI, 6PGD, PGM, PK, TPI and XO. Of these, MDH, EST and TPI are probably coded for by 2 loci each. This is suggested by widely separated mobility in multiple banded electrophoretic patterns and by independent variation between individuals of species of the two zones of each enzyme. These loci were designated in order of relative anodal mobility (e.g., mdh-1 moves more anodally than mdh-2). Twenty two presumed enzyme loci were therefore scored in total.

Of these, clear fixed differences in banding patterns were detected between

Table 15. Allele frequency from electrophoretic data for *Rossia* and *Neorossia* (N = number of specimens)

	Rossia	*Neorossia*		*Rossia*	*Neorossia*
acp			gpt		
ff		100	mm	100	100
mm	85.7		N	1	2
ms	14.3		idh		
N	7	4	mm	100	100
adh			N	7	4
mm	100		mdh-2		
N	5		mm	14.0	
ald			ms	43.0	
mm	100	100	ss	43.0	100
N	7	4	N	7	2
est-1			me		
ff	100		ff	100	
mm		66.6	mm		50.0
ms		33.3	ms		25.0
N	7	3	ss		25.0
fdp			N	7	4
mm	100	100	mpi		
N	7	1	mm	100	
fum			ss		100
mm	100		N	7	3
ss		100	pgm		
N	5	3	ff	57.1	
gapd			mf	14.3	
mm	100		mm	28.6	
ss		100	ss		100
N	4	2	N	7	4
GP			pk		
mm	100		ff	12.5	
ss		100	mf	12.5	
N	4	3	mm	75.0	
α gpd			ss		100
mm	100	100	N	8	4
N	6	2	tpi-1		
g6pdh			ff		100
mf	40.0		mm	66.6	
mm	60.0	100	ss	33.3	
N	5	3	N	5	2
gpi			xo		
mm		100	mm	100	
ss	100		ss		100
N	5	3	N	4	1

eastern Australian *Rossia* and *Neorossia* for 12 enzymes in addition to general protein stain. Diagrams of phenotypes for the enzymes for which more than one allozyme was detected is given in Figure 10. Table 15 shows allelic frequencies for each enzyme. Nei's (1972) genetic distance, D, between *Rossia* and *Neorossia* was 0.492 and between the two *Rossia* populations was 0.034.

Allozyme polymorphism was detected at three loci: pk and mdh-2 for *Rossia*, and me in *Neorossia*. Each segregated for two alleles. Presumptive fast and slow homozygotes were all single banded. Heterozygotes in *Rossia* were two banded for PGM and three banded for MDH, G6PDH and ACP suggesting monomeric and dimeric molecular structures respectively for these enzymes. At least three
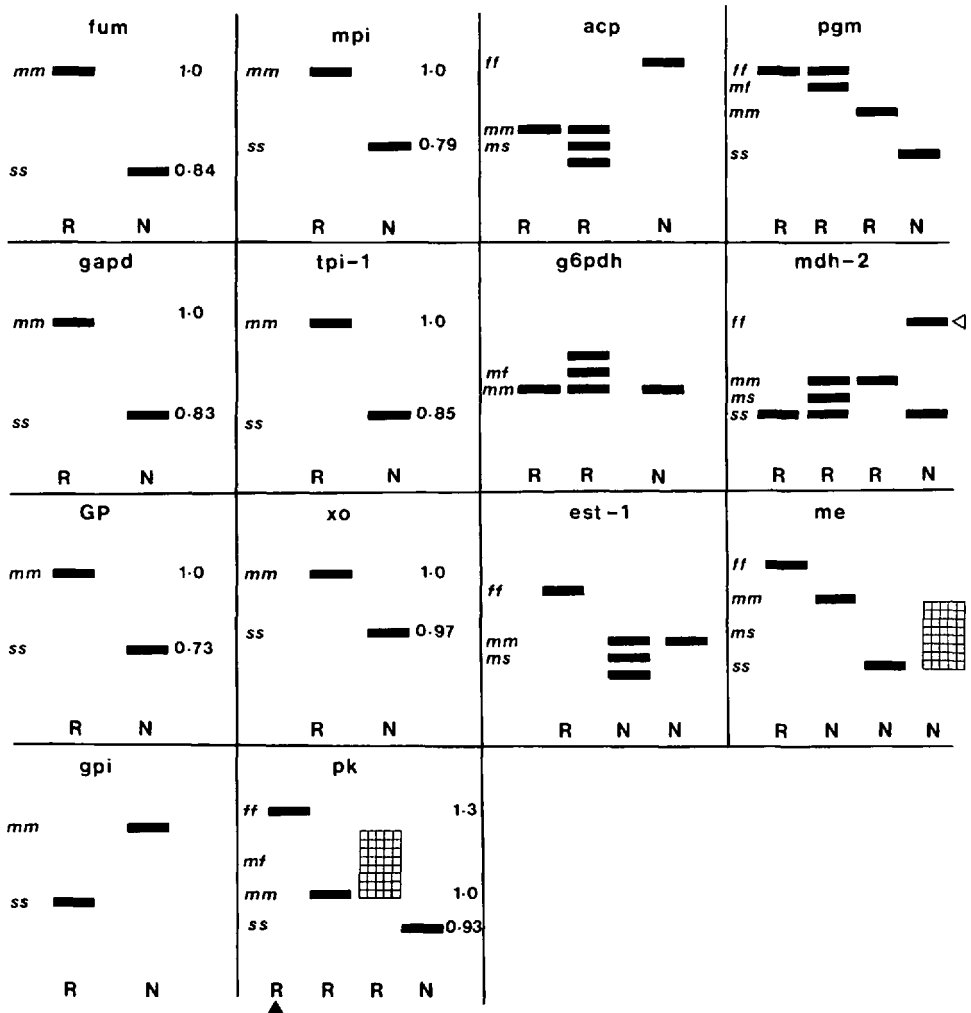
Figure 10. Diagram of the phenotypes of *Rossia* and *Neorossia* allozymes. Numerical values on the left of the diagrams refer to mobilities relative to the more frequent homozygote of the strongest allozyme. Hatched lines indicate individual bands were not resolved. The open triangle shows the position of mdh-2 (only scorable in *Neorossia*), the closed triangle indicates the only band detected for the single North West Shelf specimen.

bands were discernible in presumptive PK (*Rossia*) and ME (*Neorossia*) heterozygotes but it was not possible to identify all five bands expected from the tetrameric structure of these enzymes. *Neorossia* heterozygotes were triple banded for EST.

A single fixed gene difference in pgm was found between *Rossia* specimens from the two eastern localities. This represents a difference at 6.6% of loci. The single North West Shelf specimen showed evidence of severe protein degradation. A single band was detected for PK in a position further towards the anode than isoenzymes in other *Rossia*. However, no banding was detected for this specimen for any of the other enzymes or in the GP stain. Allelic frequencies for each enzyme for the two *Rossia* populations are given in Table 16.

Table 16. Allele frequency from electrophoretic data for eastern Australian (Sydney—S) and western Tasmanian (WT) *Rossia* (N = number of specimens showing each presumptive allelic designation)

	Rossia (S)	*Rossia* (WT)		*Rossia* (S)	*Rossia* (WT)
acp			gpt		
mm		75.0	mm	—	100
ms	100	25.0	N		1
N	3	4	idh		
adh			mm	100	100
mm	100	100	N	3	4
N	2	3	mdh-2		
ald			mm		25.0
mm	100	100	ms		75.0
N	3	4	ss	100	
est-1			N	3	4
mm	100	100	me		
N	3	4	mm	100	100
fdp			N	3	4
mm	100	100	mpi		
N	3	4	mm	100	100
fum			N	3	4
mm	100	100	pgm		
N	1	4	ff	33.3	75.0
gapd			mf		25.0
mm	—	100	mm	66.6	
N		4	N	3	4
GP			pk		
mm	—	100	mm	66.6	100
N		4	mf	33.3	
α gpd			N	3	4
mm	100	100	tpi-1		
N	2	4	mm	100	100
g6pdh			N	3	4
mf		50.0	xo		
mm	100	50.0	mm	—	100
N	1	4	N	—	4
gpi					
mm	100	100			
N	1	4			

DISCUSSION

Number of Australian *Rossia* Species

The results of the above multivariate (PCA, MANOVA and DFA) and univariate (ANOVA) analyses support the presence of two groups within the Australian *Rossia*; one group (Group 1) corresponding to a North West Shelf population and the other (Group 2) to an eastern Australian population. However, since the two groups are geographically disjunct from one another (with Group 1 at lower latitudes and longitudes), it is not possible, without further evidence, to decide whether the groups represent genetically isolated populations (allopatric species) or whether they represent portions of a single species that exhibits geographic variation (either genetically or ecophenotypically induced).

The results of the latitude and longitude regression analyses may be used to test these competing hypotheses. If a single species is involved, it would be expected that any observed geographic variation would tend to be exhibited more or less unidirectionally as trends along a given axis (e.g., latitude or longitude)

across the species range. Therefore, recalculation after the exclusion of one group from the latitudinal or longitudinal regression analyses should not result in a difference in either the significance, or a change of sign, of the correlation coefficients.

The observed effects for Group 1 exclusion did not conform to this predicted outcome. In several cases, where there had been a significant correlation with both groups combined, no correlation was observed when Group 2 specimens were analyzed separately. These results imply that the observed correlations for both groups combined are not due to clinal trends. Rather they are due to real differences between the two groups with the observed correlation simply reflecting the geographic disjunction of the samples. These results imply that the two groups represent different species.

This is also strongly supported by the lack of evidence for clinal trends as indicated by canonical variance analysis results with specimens divided into four locality groups. If a clinal trend was operating, it would be expected that the North West Shelf specimens would be more similar to southern (eastern Tasmania to the Great Australian Bight) specimens than to those remaining eastern Australian specimens. That is, the southern specimens (Group 2c) should form an intermediate cluster between the North West Shelf and remaining east coast specimens. This is clearly not the case as shown in Figure 5.

A related but even more convincing observation supporting the two species hypothesis is that of a change of sign for regression coefficients after the exclusion of the Group 1 individuals. In these, the residual values of the Group 1 individuals were opposite (to the point of pulling the regression in the opposite direction) to those predicted from the extrapolation of trends along the latitudinal and longitudinal gradients for the Group 2 individuals. It should be noted here that for one character, funnel length, such a slope reversal would also occur if a cline was operating around southern Australia. However, the preceding evidence disputes the likelihood of such a cline.

The observed lack of clustering pattern in the PCA within Group 2 samples suggests that there is only a single east Australian species. It is important to note that the lack of clustering suggests, but does not unequivocally preclude, the presence of more than one species. However, electrophoretic evidence also strongly supports the morphological evidence that *R. australis* is the only species present along the eastern Australian coast. Of the 15 enzymes for which activity was detected in both populations, only a single fixed difference was observed between specimens from eastern Australia (34°14'S, 151°29'E to 34°17'S, 151°26'E) and those from western Tasmania (37°12'S, 138°33'E to 40°41'S, 143°31'E). This represents a difference in 6.6% of loci between the two populations which falls well below the proportion of differences that would be expected should two species be present.

Identity of Australian *Rossia* Species

Comparison of Australian specimens of *Rossia* with *Rossia* from Africa further highlighted the close similarities between members of the subgenus *Austrorossia* as shown in Table 22 and discussed elsewhere.

Neither Group 1 nor Group 2 Australian species could be readily distinguished from African specimens on the basis of gross morphology and investigation of individual characters. Statistically, evidence that Group 1 and *R. mastigophora* and Group 2 and *R. mastigophora* represent in each case two populations was shown by PCA in the former case and DFA in the latter. That individuals were

consistently classified correctly lends weight to the hypothesis that the species are distinct. However, until further material is examined (including type material of *R. mastigophora* and *R. enigmatica*), and without additional evidence, it cannot be determined whether either of the identified Australian species is conspecific with the African species. The observed differences between the Australian and African species may be due to geographic variation a hypothesis that was not possible to test in this study.

For this reason, a nomenclaturally conservative approach has been adopted. As the *R. australis* paratype clusters with Group 2 when DFA scores are plotted, and since the type locality of *R. australis* (Eucla, Western Australia) falls within the range of this Group, specimens from Group 2 are assigned to *R. australis* as described by Berry (1918).

Until further consistent differences can be found between Group 1 *Rossia* and African *Rossia,* Group 1 will not be described as new and is here called *Rossia* sp. 1. An electrophoretic study is currently being undertaken to provide additional evidence in order to determine whether species recognition is warranted.

Identity of Australian *Neorossia*

A difference in a qualitative character, form of the radular teeth, between Australian *Neorossia* and *N. caroli* provides strong evidence that these two populations represent two distinct species. The radula in other cephalopod species has been shown to be extremely variable (Aldrich et al., 1971). However, in the present study, differences between the two *Neorossia* populations were consistently distinct over the range of material examined and exceeded variation observed within each disjunct population.

Although obviously distinguishable on morphological grounds, electrophoretic data comparing *Rossia* and *Neorossia* are presented here to enable comparisons to be made when further electrophoretic investigations are carried out.

KEY TO AUSTRALIAN ROSSIINAE

1a. Ink sac and anal flaps well developed. Anal pads present. Club suckers in 18–27 rows (males); 25–46 rows (females). Vane extends entire length of gladius. 2
1b. Ink sac and anal flaps greatly reduced. Anal pads absent. Club suckers in 8–10 rows. Vane present on posterior half of the gladius only. .... *Neorossia leptodons*
2a. Males HW/ClL = 1.05 – 2.64; AL IV/ClL = 1.45 – 3.06. .... *Rossia australis*
2b. Males HW/ClL = 0.64 – 0.80; AL IV/ClL = 0.87 – 1.24. .... *R.* sp. 1

Redescription of *Rossia australis* Berry
Figures 11–13, 14a, 15–17; Tables 17–20, 22; Appendix 1a

Rossia australis Berry, 1918: 252–258, pl. 69, figs. 3, 4; pl. 70, figs. 1–8; text figs. 43–47. Cotton, 1938: 388–340, figs. 1, 2. Cotton and Godfrey, 1940: 351–353, figs. 369, 370; 401–404, figs. 393–395.

Material Examined.—A complete list of material examined is given in Appendix 1a. Holotype, AMS C148246 (SSB 538, ENDEAVOUR E3636), male 32 mm ML. Paratype, USNM 815719 (SSB 537, ENDEAVOUR E3635), female 50.0 mm ML.

Description.—Mantle short, broad, cylindrical in anterior half to two-thirds, rounded posteriorly; median antero-dorsal mantle edge with low projecting crescentic margin, antero-ventral mantle edge almost straight or slightly concave, dorsal edge of mantle margin projects slightly beyond ventral edge, without distinct lobes. Fins large, ovate (FLI: males, 61.49–*72.20*–95.63; females, 50.55–*71.05*–
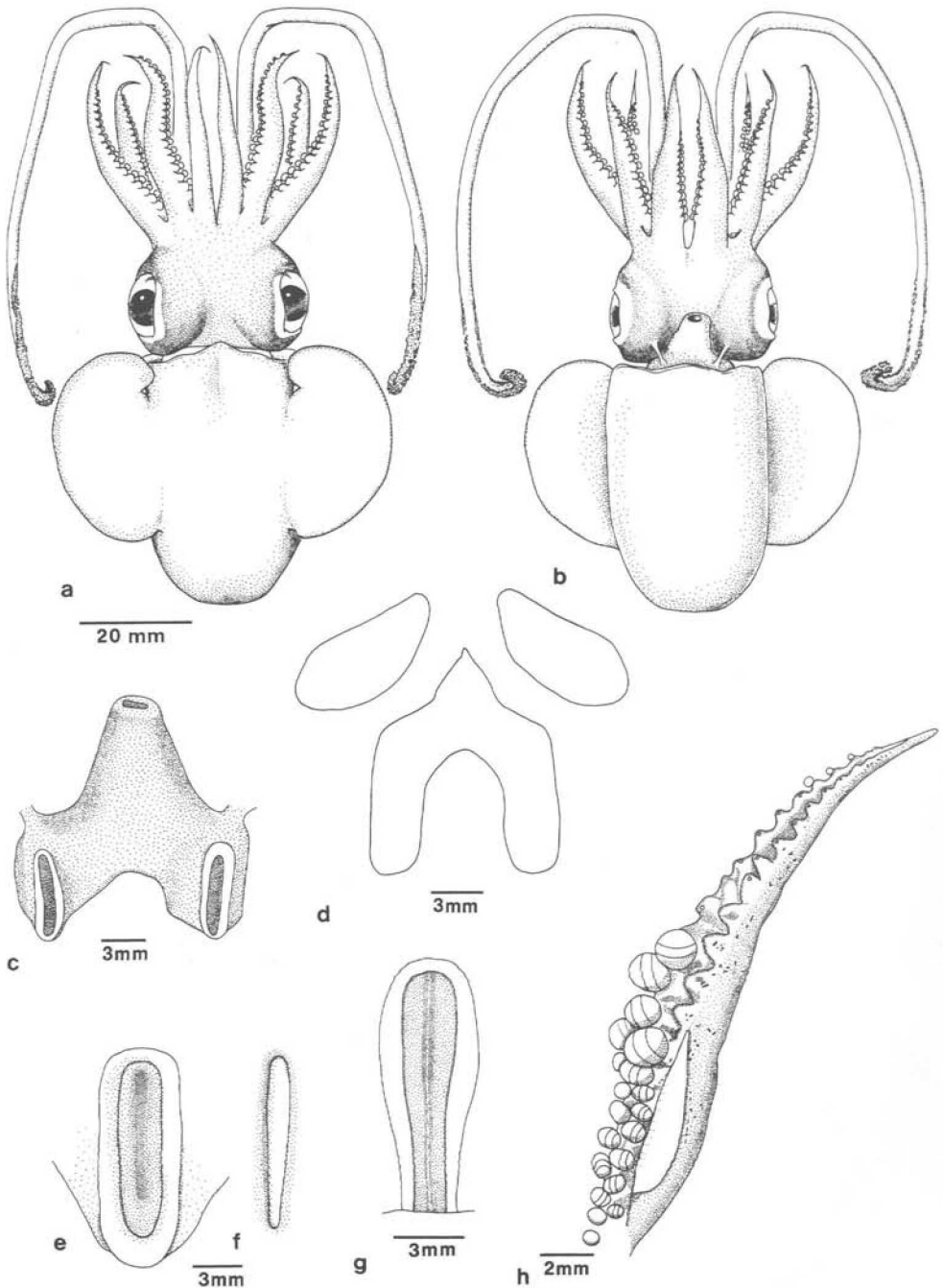
Figure 11. *Rossia australis* a) dorsal view, paratype, female, USNM 815719, 48.0 mm ML; b) ventral view, paratype, USNM 815719; c) funnel, paratype, USNM 815719; d) funnel organ, paratype, USNM 815719; e) funnel locking cartilage, female, SAM D18687, 50.7 mm ML; f) mantle locking cartilage, female, SAM D18687, g) nuchal locking cartilage, female SAM D18687; h) hectocotylus, left Arm I, MV F57479, 24.5 mm ML.
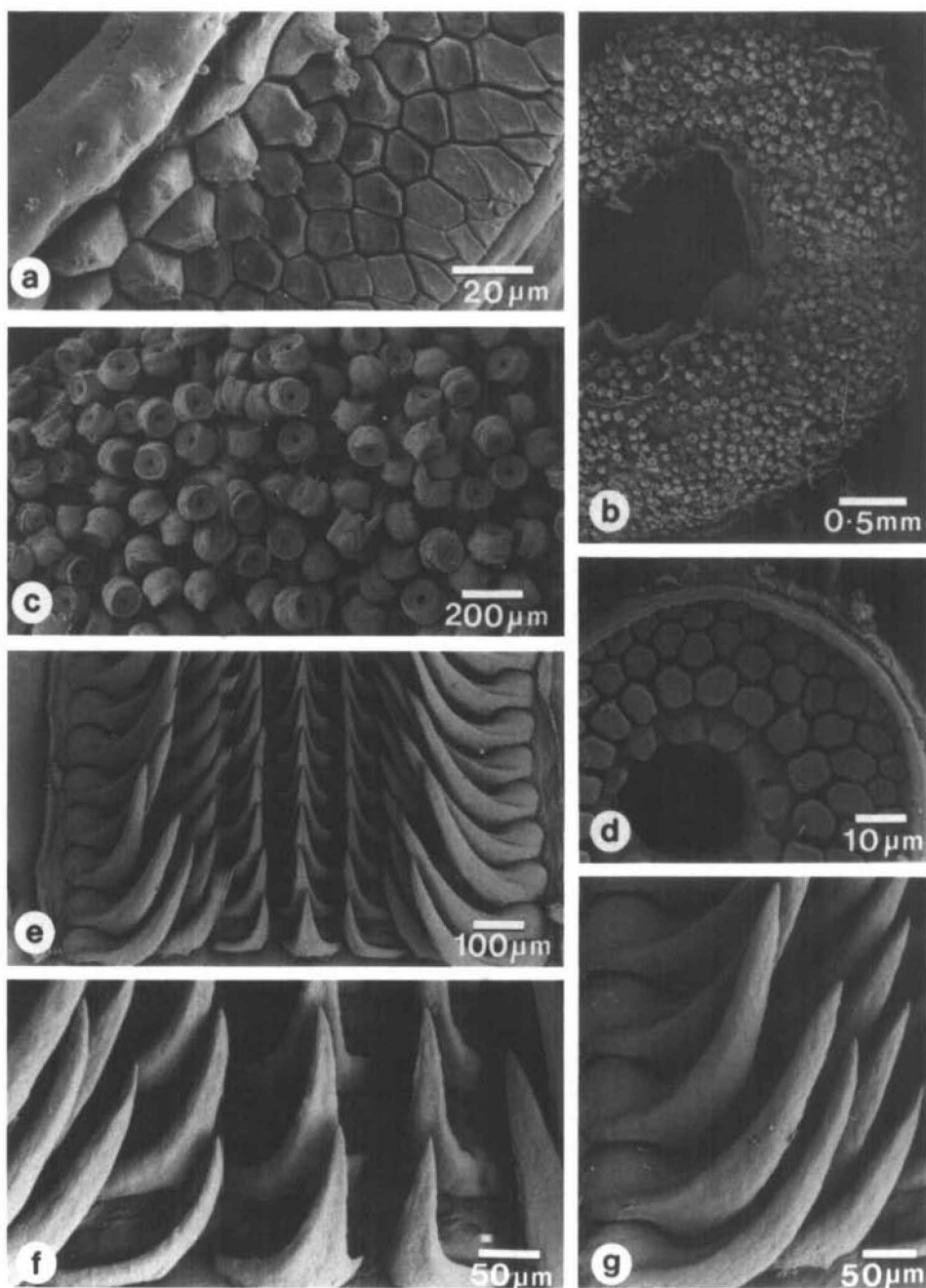
Figure 12. *Rossia australis* a) arm sucker rim (Arm III), female, MV F57457, 49.7 mm ML; b) club, distalmost end, male, MV F57479, 24.5 mm ML; c) club suckers, female, AM C161431, 32.3 mm ML; d) club sucker rim, female, AM C161431; e) radula, male, AM C105864, 37.0 mm ML; f) radula, left to right: 2nd lateral, 1st lateral, rhachidian teeth, male, AM C105864; g) radula, left to right: 3rd and 2nd lateral teeth, male, AM C105864.
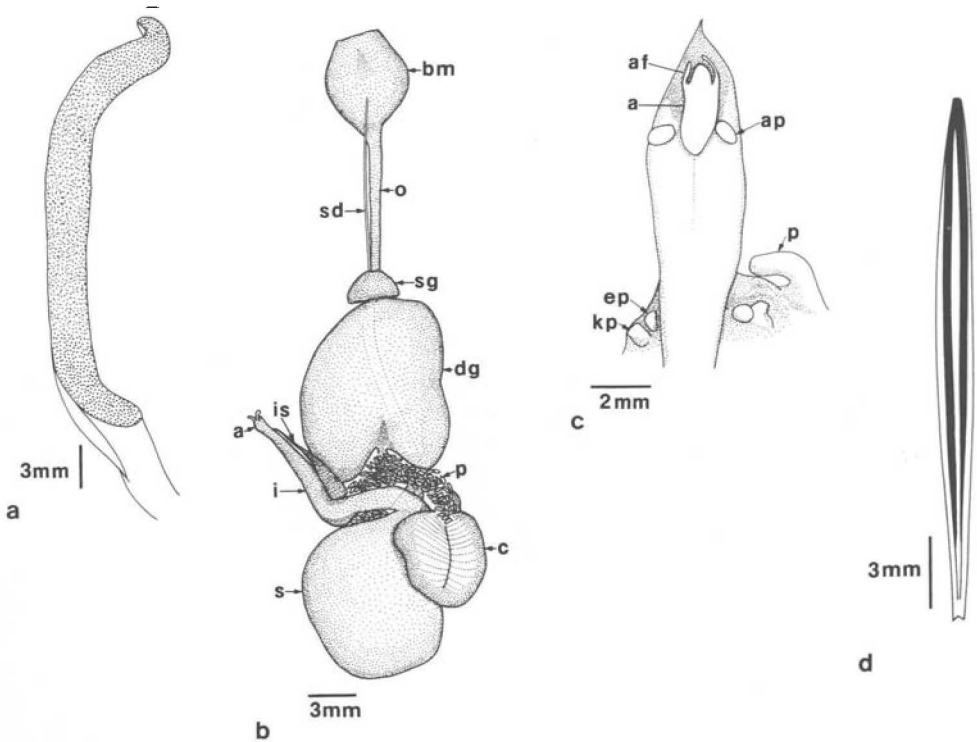
Figure 13. *Rossia australis* a) left tentacular club, female, AM C161423, 35.9 mm ML; b) digestive tract, ventral view, male, AM C161440, 27.2 mm ML (a—anus, bm—buccal mass, c—caecum, dg—digestive gland, i—intestine, is—ink sac, o—esophagus, p—pancreas, s—stomach, sd—salivdary duct, sg—salivary gland); c) portion of anterior mantle organ complex, male, MV F58479, 24.5 mm ML (a—anus, af—anal flap, ap—anal pad, ep—epirenal body, kp—kidney papilla, p—penis); d) gladius (anterior—top, posterior—bottom), female, AM C161426, 43.0 mm ML.

88.85. FWSI: males, 30.60–*41.98*–53.65; females, 25.26–*40.97*–71.10), attached dorso-laterally within anterior two-thirds of mantle; posterior margins curved; anterior margins convex with well-developed lobes, indented at point of fin insertion, lateral lobes broadly rounded. Anterior edge of fins extends approximately to level of mantle opening (Fig. 11a, b).

Funnel conical and broad based, tapering and projecting anteriorly approximately to level of middle of eye, free for most of its length (Fig. 11c). Funnel valve prominent, rounded anteriorly. Dorsal funnel organ large; median limbs with broad, blunt lobes, slightly tapered posteriorly, V-shaped anteriorly with simple, pointed terminal apical papilla; ventral pads ovoid, slightly broader posteriorly, medial and lateral borders usually curved, convex or sometimes slightly concave (Fig. 11d). Funnel locking cartilage a deep straight groove, ovoid anteriorly with entire margin flattened forming a broad rim (Fig. 11e). Mantle locking cartilage a slightly-curved, narrow ridge (Fig. 11f).

Head slightly broader than long in both sexes (mean HW/HL = 117%), equal to or slightly broader than mantle in females, usually wider than mantle in males (mean HW/MW: males, 125%; females, 106%), with slight median depression dorsally. Eyes large and bulbous (EDI: males, 26.00–*53.03*–67.81; females, 29.51–*51.77*–68.30); ventral eyelids free; a small oval olfactory pore present laterally on
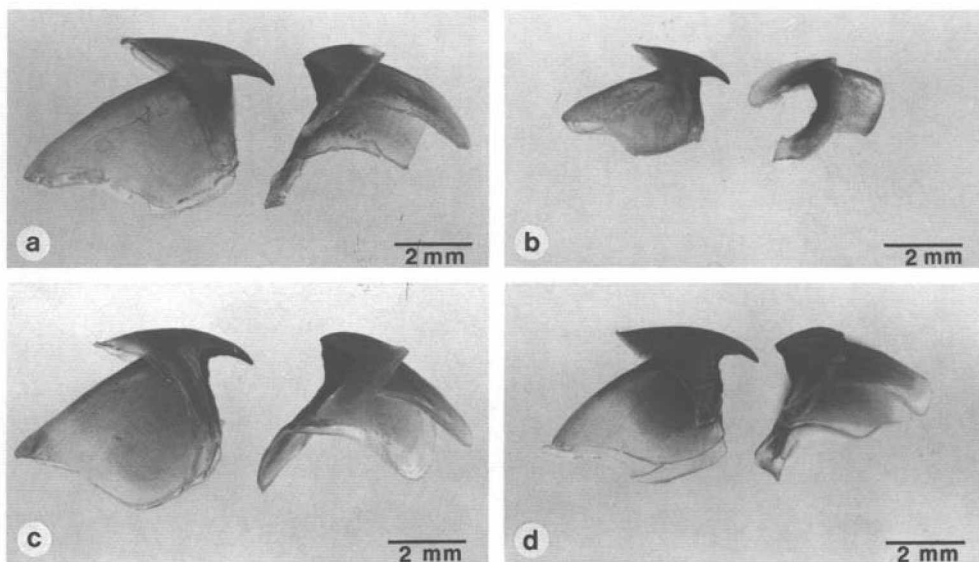
Figure 14. a) *Rossia australis* upper beak (left), lower beak (right), male, AM C161426, 28.2 mm ML. b) *Rossia* sp. 1 upper beak (left), lower beak (right), male, FV F57496, 29.6 mm ML. c) *Neorossia caroli* upper beak (left), lower beak (right), male, MV F54940, 34.7 mm ML. d) *Neorossia leptodons* n. sp. upper beak (left), lower beak (right), male, AM C161460, 36.1 mm ML.

posterior surface of eye in a position in line with the junction of second and third arms. Nuchal locking cartilage (Fig. 11g) elongate, oval rounded anteriorly, tapering, slightly narrower posteriorly, sides approximately parallel, with wide outer rim and distinct median furrow (mean NCL/NCW: males, 2.90; females, 3.17).

Arms robust, broad basally, tapering distally; order variable, however arms I and IV usually shorter than II and III. Arm formula usually III:II:IV:I or II:III: IV:I. All arms similar in shape, semicircular to subtriangular in section, with indistinct keels present on median aboral sides of arms II, III and IV. Dorsal arms narrower than remaining arms. Sucker pedicels short, each with small bilobed tubercles on external face forming a shallow scalloped protective membrane. Arm suckers biserial, spherical throughout. Largest suckers of arms II and III larger than those of arms I and IV in both sexes. In females, suckers smallest at arm bases, enlarged along middle portion of arms, abruptly diminish in size from the distalmost third to the tip. Suckers not enlarged to extent seen in males (Fig. 17k–n, Table 18). Arm sucker dentition. Chitinous rims of all arm suckers with smooth inner ring. Infundibulum with 5–7 rows of hexagonal processes with blunt pegs. Pegs often worn in mature specimens, but traces of pegs usually visible on inner plate rows. Peripheral sucker rim processes radially arranged, elongate, without pegs (Fig. 12a). Hectocotylus. Dorsal arm pair of males hectocotylized (Fig. 11h). Ventro-lateral edge of oral surface bordered by swollen glandular crest, the inner edge of which forms a deep furrow extending from sucker rows 4–6 to 8–11 (usually 4–9). First 8–10 sucker rows from base row small, next 4–8 rows enlarged, remaining suckers gradually diminish in size distally.

Tentacles long, slender, stalks naked, length 1–4 times ML; semicircular in section; oral surface flattened with groove extending to club base. Club (Figs. 12b, 13a) not expanded, diameter uniform through most of length, tip tapers to blunt end distally. Suckers 0.10 mm diameter in center of club, 0.12 mm diameter at
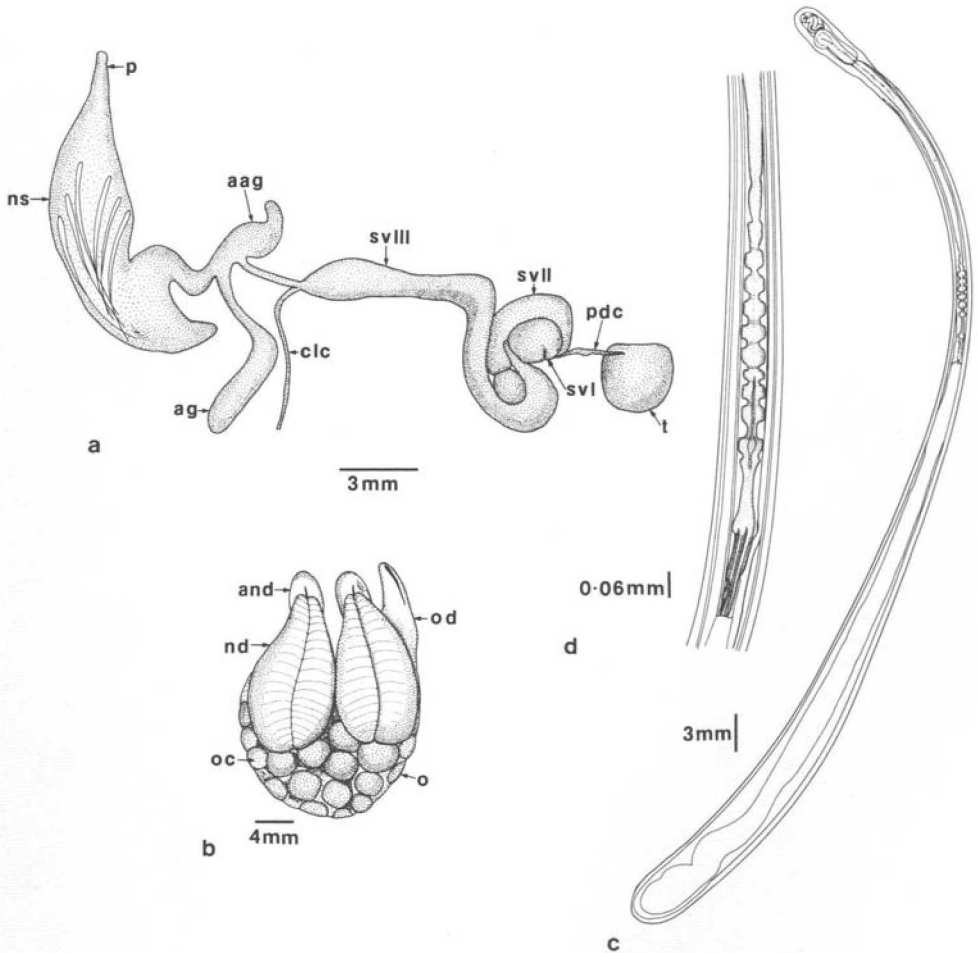
Figure 15. *Rossia australis* a) male reproductive organs, AM C161431, 23.3 mm ML (ag—accessory gland, aag—appendage of accessory gland, clc—ciliated canal, ns—Needhams sac, p—penis, pdc—proximal deferent canal, sv I–III—seminal vesicles I, II, III, t—testis); b) female reproductive organs, ventral view, paratype, USNM 815719, 50.0 mm ML, (and—accessory, nidamental gland, nd—nidamental gland, o—ovary, oc—oocyte, od—oviduct); c) whole spermatophore, MV F57479, 24.5 mm ML; d) portion of oral end of spermatophore, base of ejaculatory apparatus connected to sperm reservoir, MV F57479.

either end of club (CLRC: males, 18–*22*–26; females, 25–*30*–33). Narrow swimming keel on aboral side of carpus extends from a point approximately 1 cm proximal to club along its entire length. Proximal third of keel widest. Club sucker dentition. Inner ring with 9–12 blunt projections. Infundibulum with 4–5 rings of round-ovate polygonal processes without pegs. At periphery, polygonal processes smaller, subrectangular (Fig. 12c, d).

Buccal membrane with six lappets, without suckers. Buccal connectives extend to level of first or second sucker row. Beak. Chitin of upper and lower beaks black, darkening gradually from rostrum to hood, crest and lateral walls. Upper beak with long pointed and slightly curved rostrum. Lateral wall edge with deep depression. Crest wide. Lower beak has slightly curved rostral edge. Jaw angle distinct; obtuse. No indentation at lateral wall edge. Hood notch broad, deep.
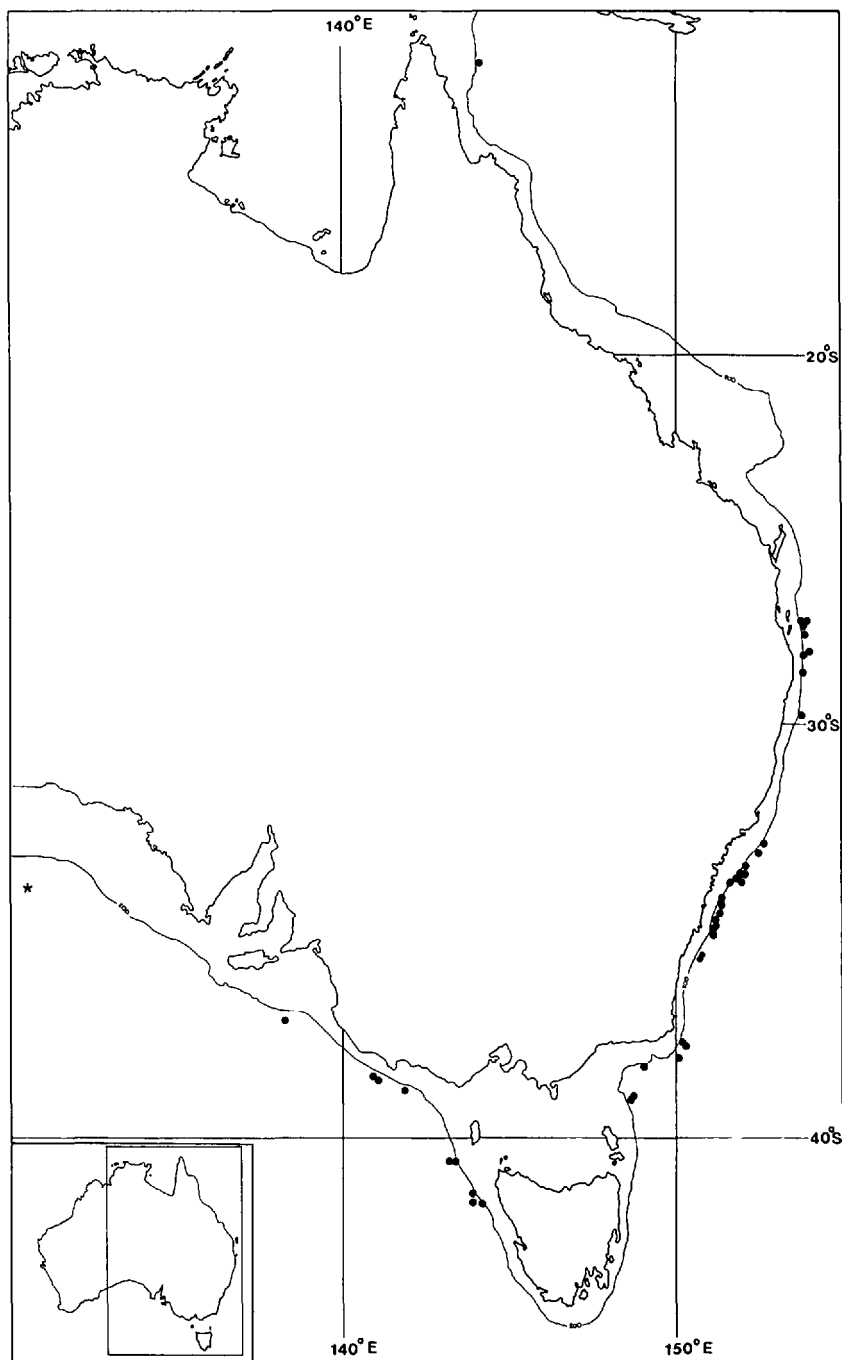
Figure 16.   Distribution of *Rossia australis*. Dots indicate collection sites of specimen lots examined in this study, * indicates type locality.
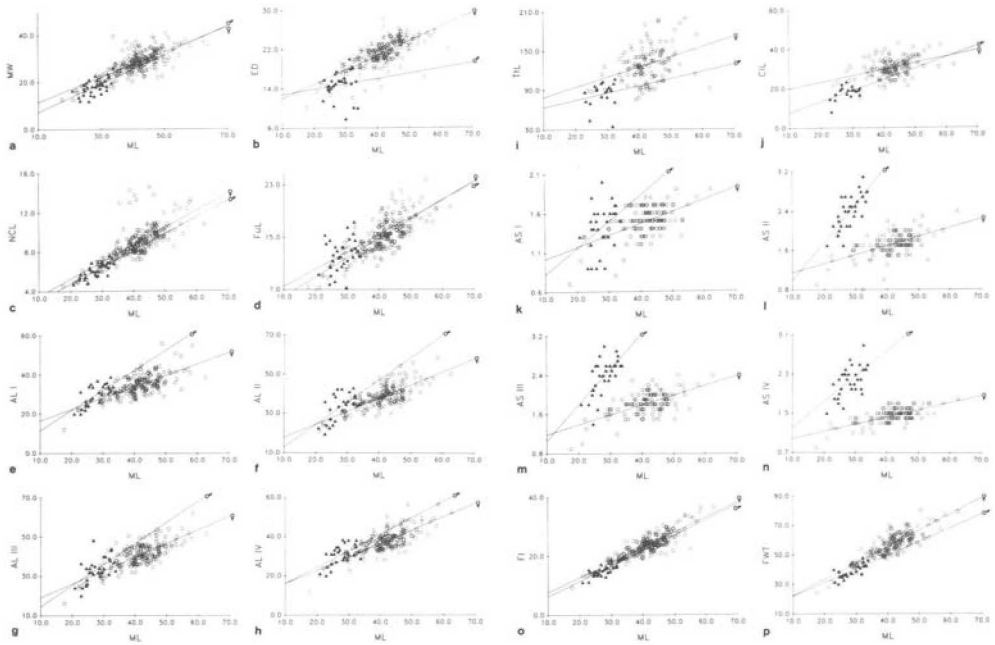
Figure 17. Sexual dimorphism in *Rossia australia*. For regression formulae and comparison of lines refer to Table 17. Abbreviations for characters are given in Table 1. Solid triangles = males, open circles = females.

Wings widely spread. Rostrum protrudes forward slightly. Wing fold rounded, thickened slightly. Shoulder distinct, without groove, small tooth sometimes present (often worn). Jaw sharp edged and thickened. Crest broad in section (Fig. 14a). Radula with seven transverse rows of teeth. Rhachidian teeth broad-based, without cusps, tapering, fine triangular. First lateral teeth, narrow triangular, with wide heel, asymmetrical with tooth displaced toward the midline of the radula. Second and third lateral teeth long, sabre-like, with short base. Third laterals usually rounded at the base and strongly indented. Outer face of tooth rounded with curved ridge developed. Marginal plates absent (Fig. 12e–g). Of 4 males (mean ML 28.9 ± 1.3 mm) and 14 females (mean ML 42.4 ± 7.8 mm), average rhachidian tooth size less in males (mean RL: males 136.5 ± 47.5 μm; females 224.8 ± 40.6 μm).

Digestive System (Fig. 13b).—Single broad, semicircular salivary gland, close to anterior end of digestive gland. From it a single salivary duct runs forward alongside esophagus to enter buccal mass in ventral-mid line. Esophagus runs dorsally along midline of digestive gland, broadening as it enters stomach immediately below posterior end of digestive gland. Stomach a large globose sac, thin posteriorly and with broad muscular band anteriorly encircling stomach transversely. Caecum circular in outline; disc-like, narrow, grooved in a blunt V anteriorly; surface lining finely pleated. A single duct connects digestive gland near midline with stomach and caecum. Digestive gland large, globular, divided posteriorly into two large subtriangular lobes. Intestine short, wide and undifferentiated. Ink sac large, attached dorsally to intestine and opening into it via a short, narrow duct just behind anal opening on dorsal side. Ink sac and posterior intestine lie superficially in a groove on the ventral face of digestive gland. Digestive gland

Table 17. Morphological parameters showing sexual dimorphism in *Rossia australis*. Regression data relating to figures where $Y = a + bX$ where Y = dependent variable, a = intercept, b = slope, X = ML, Sig. = significant difference between the regression lines of males (M) and females (F) with respect to slope or intercept (int.); *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant. (Significance of individual regression lines the same in all cases: $P < 0.001$). r^2 = proportion of total variation accounted for by regression

Y	Sex	N	r^2	a	b	Sig.
MW	M	33	0.383	1.08	0.609	*** (int.)
	F	204	0.527	6.09	0.532	
ED	M	28	0.016	11.74	0.107	*** (int.)
	F	198	0.513	9.05	0.291	
NCL	M	33	0.593	1.34	0.170	* (int.)
	F	205	0.529	1.76	0.174	
FuL	M	32	0.134	4.85	0.264	* (int.)
	F	198	0.562	3.10	0.293	
AL I	M	28	0.496	1.27	1.026	* (slope)
	F	171	0.489	10.59	0.583	
AL II	M	27	0.380	1.47	1.142	*** (int.)
	F	163	0.548	11.03	0.672	
AL III	M	29	0.356	3.83	1.069	* (int.)
	F	171	0.577	12.12	0.689	
AL IV	M	28	0.337	7.60	0.834	** (int.)
	F	172	0.623	9.19	0.675	
TtL	M	19	0.032	52.53	1.093	** (int.)
	F	116	0.130	63.44	1.541	
ClL	M	18	0.252	2.01	0.563	*** (int.)
	F	122	0.164	16.71	0.324	
AS I	M	28	0.139	0.48	0.033	** (int.)
	F	119	0.312	0.87	0.015	
AS II	M	30	0.534	0.21	0.077	*** (slope)
	F	114	0.310	0.97	0.018	
AS III	M	31	0.424	0.33	0.073	* (slope)
	F	114	0.369	0.98	0.020	
AS IV	M	31	0.335	0.68	0.053	*** (slope)
	F	116	0.839	0.84	0.015	
FI	M	33	0.675	0.97	0.552	* (int.)
	F	202	0.750	2.41	0.512	
FWT	M	27	0.461	12.58	0.925	** (int.)
	F	151	0.721	11.20	1.104	

duct with branching, attached pancreatic tissue throughout. Anus with well-developed paired anal flaps. Paired anal pads of unknown function present in both sexes. Pads appear to be of glandular nature, ovoid, lie either side of rectum just behind anal opening. In males paired epirenal bodies present, lie proximal and slightly anterior to kidney papillae (Fig. 13c). Gladius visible through mantle integument in anterior third, slightly shorter than length of mantle, extends anteriorly to mantle edge. Rachis extends almost to posterior tip of vane, approximately equal width throughout most of its length, tapering, in posterior third of gladius to a fine point. Vane lanceolate, extending full length of gladius, approximately equal to median thickened rachis margin in width throughout most of its length (though variable, vane relatively broader in larger specimens), tapers markedly anteriorly, terminates in a V-shaped tip posteriorly (Fig. 13d).

Reproductive System. — MALES. Testis on left posterior side of viscero-pericardial coelom below and close to caecum. At distal end, convoluted proximal deferent

canal (Fig. 15a) opens into a lobe shaped seminal vesicle I. This is connected with seminal vesicle II, composed of a cylindrical part with a rounded appendage. Seminal vesicle III long, S-shaped, joins a delicate ciliated canal (which opens into genital sac) and a narrow tube which connects accessory gland and accessory gland appendage. Accessory gland appendage joins posterior end of Needhams sac via the distal deferent canal. Needhams sac large, leaf shaped, the posterior end produced into a large tongue-shaped lobe. Genital orifice opens into anterior end of mantle cavity. Spermatophores long (SpLI = 20.0–*27.63*–34.93) and slender (SpWI = 1.33–*1.72*–2.18). Aboral end of spermatophore widest with sperm reservoir tapering, gradually over the first third, then abruptly to where connective attaches (Fig. 15c). Structure of ejaculatory apparatus simple, connected directly to end of sperm reservoir. Middle tunic of ejaculatory apparatus highly convoluted at base then expanded in a series of ovoid disc shaped structures connected by narrow necks (Fig. 15d). These structures become less strongly delineated toward oral end of spermatophore, giving the membrane a wavy appearance. Oral end dilated enclosing remainder of loosely coiled ejaculatory apparatus. Entire sperm reservoir and ejaculatory apparatus surrounded by a double membrane.

FEMALES. Ovary large, occupies large proportion of posterior end of mantle cavity, displacing other organs when mature. Contains oocytes of various sizes, largest round, translucent with mean diameter 9.5 mm. Opens via single thick walled oviduct at anterior end on the left side. Opening of oviduct modified as a seminal receptacle, often with spermatophores embedded on inner edge of opening to oviduct, giving a granular appearance. Paired tear-shaped nidamental glands occupy a position ventral to ovary toward anterior end. Inverted U shaped accessory nidamental glands are located toward distal end of nidamental glands (Fig. 15b).

Color in alcohol cream with pink to maroon chromatophores, distributed evenly over mantle, head and arms, slightly darker and more concentrated on the dorsal surface, particularly about the eyes. Ventral surface of fins with a broad band of chromatophores closest to junction of fin and mantle and a thin band around outer fin edges. Remaining surface without chromatophores.

Size at Maturity. — Males mature at smaller sizes and do not grow as large as the females. (ML: males, 20.9–*27.81*–33.8 mm; females, 17.6–*41.3*–62.6 mm). The smallest male in which spermatophores were found was 22.9 mm ML. Females of ML > 30 mm, NDL/NDW 1.35–2.25, NDL > 11.3 mm were found to contain well-developed eggs in the ovary. A few females > 30 mm ML did not contain eggs and it is presumed they had been recently deposited, as in all cases the nidamental gland exceeded 12 mm in length. Mature specimens of both sexes were collected throughout the year. Immature specimens were collected primarily from October–January.

Type Locality. — Western Australia, Great Australian Bight, south of Eucla —°—'S, 130°50'E, 250–300 fm (457–548 m). The latitude is not given in the original description. Locality of Eucla 34°41'S, 128°52'E.

Distribution. — Australia: Queensland, Raine Island 11°35'S, 144°04'E to Western Australia, Great Australian Bight, approximately 34°S, 130°50'E (Fig. 16). Depth range 131–665 m.

Remarks. — The holotype (AMS C148246) is a badly dehydrated male specimen in very poor condition and was unsuitable for diagnostic purposes. One female paratype, 50 mm ML (SSB 539, E3637), recorded in the original description could

Table 18. Ranges, means and standard deviations of measurements and indices of *Rossia australis*, *R.* sp. 1 and *R. mastigophora* males and females

Index/Measure	Males			Females		
	R. australis	*R.* sp. 1	*R. mastigophora*	*R. australis*	*R.* sp. 1	*R. mastigophora*
ML (N, range) ($\bar{x} \pm$ SD)	33, 20.9–33.8 (27.81 ± 3.45)	12, 19.6–35.1 (29.13 ± 5.20)	3, 29.1–37.2 (31.87 ± 4.62)	205, 17.6–62.6 (41.37 ± 7.12)	22, 28.5–65.6 (48.10 ± 10.46)	11, 30.0–59.7 (46.54 ± 7.94)
MWI	33, 45.2–80.5 (64.86 ± 9.75)	12, 45.1–74.0 (62.94 ± 9.23)	3, 47.3–65.9 (56.05 ± 9.33)	204, 45.5–115.5 (68.41 ± 8.98)	22, 40.4–89.7 (72.53 ± 12.27)	11, 52.7–76.7 (63.20 ± 7.67)
HLI	32, 51.3–95.7 (69.01 ± 8.91)	12, 59.4–81.1 (68.87 ± 6.97)	3, 56.3–66.0 (60.66 ± 4.91)	200, 38.4–87.9 (62.66 ± 8.03)	22, 46.4–85.0 (67.63 ± 8.95)	11, 49.4–72.3 (55.49 ± 6.05)
HWI	26, 51.0–110.5 (81.81 ± 12.31)	12, 51.0–75.8 (69.48 ± 6.91)	3, 69.1–84.2 (77.37 ± 7.66)	185, 55.7–102.9 (73.54 ± 8.95)	21, 50.6–83.3 (68.63 ± 10.45)	11, 56.4–94.3 (64.92 ± 10.60)
EDI	28, 26.0–67.8 (53.03 ± 10.28)	12, 38.2–56.2 (45.56 ± 5.83)	3, 47.3–56.7 (52.30 ± 4.70)	198, 29.5–68.3 (51.77 ± 6.33)	22, 34.2–58.2 (44.52 ± 6.87)	11, 40.5–60.3 (45.34 ± 6.03)
NCLI	33, 17.6–25.8 (21.84 ± 1.84)	12, 14.9–22.6 (19.59 ± 2.45)	3, 14.5–19.6 (17.89 ± 2.96)	205, 16.2–36.7 (21.78 ± 2.93)	22, 14.0–23.3 (19.82 ± 2.35)	11, 19.1–22.6 (20.98 ± 1.27)
NCWI	32, 5.7–10.5 (7.66 ± 1.05)	12, 5.7–8.1 (6.68 ± 0.82)	3, 6.8–8.3 (7.57 ± 0.75)	204, 2.7–11.0 (7.16 ± 1.21)	22, 4.7–8.1 (6.63 ± 0.99)	11, 6.7–9.4 (7.73 ± 0.82)
NCL/NCW	32, 2.2–4.3 (2.90 ± 0.47)	12, 2.1–3.7 (2.97 ± 0.47)	3, 2.1–2.6 (2.35 ± 0.23)	204, 2.0–11.8 (3.17 ± 1.02)	22, 2.3–4.0 (3.03 ± 0.48)	11, 2.3–3.2 (2.74 ± 0.30)
FuLI	32, 24.7–66.8 (44.07 ± 8.84)	12, 36.1–60.5 (46.78 ± 7.10)	3, 35.7–47.4 (41.95 ± 5.87)	198, 26.8–50.9 (37.04 ± 4.69)	22, 32.8–59.0 (44.04 ± 6.33)	11, 31.8–52.3 (36.81 ± 5.84)
ALI I	28, 87.3–136.7 (107.2 ± 14.4)	9, 72.9–121.6 (100.9 ± 4.0)	3, 82.5–116.0 (96.64 ± 17.39)	171, 58.6–114.8 (84.58 ± 10.84)	18, 76.7–120.2 (93.81 ± 10.33)	9, 70.2–84.2 (76.87 ± 4.94)
ALI II	27, 85.2–158.2 (119.5 ± 20.6)	10, 97.2–123.2 (112.5 ± 8.5)	3, 99.5–129.7 (109.6 ± 17.4)	163, 68.5–121.1 (94.65 ± 11.00)	17, 86.7–114.4 (99.99 ± 9.69)	8, 75.2–110.0 (85.61 ± 10.68)
ALI III	29, 87.3–180.2 (120.8 ± 19.3)	11, 86.8–128.2 (112.3 ± 13.3)	3, 96.2–136.5 (109.8 ± 23.1)	171, 75.5–138.2 (98.97 ± 11.56)	19, 79.4–139.3 (103.4 ± 15.3)	10, 81.7–120.0 (95.12 ± 11.26)
ALI IV	28, 84.9–136.2 (111.3 ± 15.4)	10, 83.7–111.1 (97.54 ± 7.94)	3, 80.6–109.2 (91.92 ± 15.20)	172, 66.7–118.5 (90.56 ± 10.36)	18, 71.2–139.3 (97.64 ± 16.15)	9, 70.5–113.3 (81.30 ± 12.96)
TtLI	19, 109.8–378.2 (296.0 ± 66.9)	5, 236.3–481.9 (365.7 ± 90.8)	2, 233.7–250.0 (241.8 ± 11.5)	116, 147.0–450.2 (306.3 ± 61.3)	17, 228.7–560.1 (353.2 ± 82.6)	11, 196.4–433.3 (275.2 ± 65.7)
CILI	18, 34.3–82.6 (63.45 ± 11.36)	5, 84.2–115.9 (98.85 ± 12.37)	2, 78.0–92.8 (85.37 ± 10.48)	122, 44.6–105.9 (72.53 ± 12.83)	17, 61.8–135.4 (99.26 ± 20.30)	11, 47.8–110.0 (63.37 ± 19.29)
ASIn I	28, 3.1–7.3 (5.11 ± 1.05)	12, 2.9–4.7 (3.91 ± 0.46)	3, 3.8–6.8 (5.13 ± 1.56)	119, 2.4–5.9 (3.65 ± 0.62)	12, 2.3–4.9 (3.72 ± 0.75)	11, 2.7–5.7 (3.44 ± 0.80)

Table 18. Continued

Index/Measure	Males			Females		
	R. australis	R. sp. 1	R. mastigophora	R. australis	R. sp. 1	R. mastigophora
ASIn II	30, 6.5–10.6 (8.52 ± 0.88)	12, 5.1–7.4 (6.28 ± 0.77)	3, 6.9–10.2 (8.03 ± 1.91)	114, 2.5–8.0 (4.25 ± 0.79)	13, 2.6–5.6 (4.03 ± 0.84)	10, 3.3–6.3 (3.97 ± 0.88)
ASIn III	31, 5.7–10.6 (8.48 ± 1.07)	12, 4.5–7.4 (6.11 ± 0.90)	3, 7.5–10.9 (8.67 ± 1.95)	114, 3.0–6.8 (4.45 ± 0.69)	12, 3.2–6.0 (4.42 ± 0.79)	10, 3.5–6.3 (4.21 ± 0.81)
ASIn IV	31, 5.9–9.2 (7.73 ± 0.93)	10, 3.6–5.9 (5.14 ± 0.78)	3, 6.6–9.2 (7.01 ± 1.92)	116, 2.6–5.9 (3.57 ± 0.56)	11, 2.2–4.6 (3.28 ± 0.76)	8, 2.5–3.3 (2.91 ± 0.28)
CISI	18, 0.31–0.44 (0.35 ± 0.42)	4, 0.26–0.42 (0.33 ± 0.06)	2, 0.32–0.34 (0.33 ± 0.01)	110, 0.16–0.42 (0.24 ± 0.04)	15, 0.15–0.36 (0.23 ± 0.06)	11, 0.17–0.67 (0.25 ± 0.14)
FPI	31, 12.6–26.3 (18.50 ± 3.72)	12, 17.1–24.7 (20.49 ± 2.67)	3, 18.2–43.3 (29.01 ± 13.40)	195, 9.3–37.2 (15.96 ± 3.77)	22, 12.6–24.8 (20.28 ± 3.30)	11, 11.5–19.3 (16.18 ± 2.87)
FII	33, 45.7–66.8 (55.70 ± 4.68)	12, 50.3–63.2 (57.11 ± 4.10)	3, 55.0–56.2 (55.71 ± 0.64)	202, 40.7–71.5 (57.23 ± 4.96)	22, 49.6–72.0 (59.69 ± 5.65)	11, 52.8–67.3 (61.11 ± 4.55)
FLI	33, 61.5–95.6 (2.20 ± 6.52)	12, 58.2–82.8 (71.05 ± 6.65)	3, 63.7–74.1 (68.38 ± 5.25)	198, 50.5–88.8 (71.05 ± 6.75)	21, 63.7–86.4 (73.15 ± 5.86)	11, 59.1–81.0 (74.49 ± 6.19)
FWSI	33, 30.6–53.6 (41.98 ± 4.65)	11, 31.2–45.6 (41.25 ± 4.16)	3, 34.4–51.9 (41.82 ± 9.03)	199, 25.3–71.1 (40.97 ± 5.61)	21, 35.9–55.2 (43.77 ± 5.35)	11, 30.6–50.7 (41.56 ± 5.87)
FWTI	27, 116.1–174.7 (137.6 ± 13.5)	11, 114.2–152.3 (133.2 ± 9.4)	3, 107.5–140.3 (125.8 ± 16.7)	151, 111.3–172.2 (138.2 ± 12.2)	18, 122.0–169.4 (146.0 ± 13.8)	10, 126.8–150.3 (140.2 ± 8.0)
FL/FW	33, 1.35–2.19 (1.73 ± 0.20)	11, 1.3–2.1 (1.74 ± 0.22)	3, 1.4–1.8 (1.67 ± 0.22)	195, 1.0–2.9 (1.76 ± 0.26)	21, 1.3–2.0 (1.69 ± 0.17)	11, 1.6–2.0 (1.81 ± 0.15)
EgDI				171, 4.5–14.6 (9.53 ± 1.84)	14, 4.9–13.9 (8.43 ± 2.49)	10, 6.7–11.9 (9.57 ± 1.51)
NDLI				205, 12.5–59.2 (42.11 ± 6.82)	22, 26.7–60.4 (46.39 ± 6.49)	11, 26.7–50.9 (43.20 ± 7.19)
NDWI				203, 2.8–36.3 (24.23 ± 5.87)	21, 8.4–34.3 (24.57 ± 7.35)	11, 8.0–28.9 (23.82 ± 5.74)
SpLI	25, 20.0–34.9 (27.63 ± 3.47)	8, 17.3–29.4 (22.40 ± 3.70)	2, 26.9–30.7 (28.80 ± 2.71)			
SpWI	25, 1.33–2.18 (1.72 ± 0.23)	8, 1.2–1.8 (1.47 ± 0.24)	2, 1.3–1.7 (1.52 ± 0.26)			

Table 19. Ranges, means and standard deviations of meristic variables for *Rossia australis*, *R.* sp. 1 and *R. mastigophora* males and females

| Count	Males			Females		
	R. australis	*R.* sp. 1	*R. mastigophora*	*R. australis*	*R.* sp. 1	*R. mastigophora*
CIRC (N, range) ($\bar{x} \pm$ SD)	17, 18–26 (21.71 ± 2.59)	5, 22–27 (24.20 ± 2.17)	2, 30–35 (32.50 ± 3.54)	93, 25–33 (29.82 ± 1.81)	13, 33–46 (36.92 ± 4.23)	11, 23–40 (26.55 ± 5.11)
ASC I	29, 16–27 (21.69 ± 2.41)	12, 17–25 (20.33 ± 2.31)	3, 20–23 (21.00 ± 1.73)	193, 17–26 (21.30 ± 1.78)	19, 16–24 (20.58 ± 2.34)	11, 17–23 (20.55 ± 2.07)
ASC II	32, 12–21 (17.12 ± 1.90)	11, 14–18 (15.91 ± 1.37)	3, 16–19 (18.00 ± 1.73)	186, 17–27 (21.06 ± 1.73)	17, 18–24 (20.18 ± 1.67)	10, 19–23 (20.80 ± 1.23)
ASC III	31, 13–23 (17.29 ± 2.40)	10, 14–20 (15.90 ± 1.79)	3, 16–18 (17.33 ± 1.15)	189, 17–27 (20.62 ± 1.69)	20, 15–24 (20.35 ± 2.50)	11, 18–23 (20.73 ± 2.00)
ASC IV	33, 13–23 (17.94 ± 2.32)	11, 14–20 (17.27 ± 1.74)	3, 18–20 (19.00 ± 1.00)	193, 17–28 (21.50 ± 1.92)	20, 17–24 (20.65 ± 1.98)	11, 19–24 (21.27 ± 1.68)
ASCT I	9, 32–72 (58.56 ± 13.51)	11, 37–61 (52.27 ± 6.74)	2, 59–64 (61.50 ± 3.54)	38, 43–92 (72.61 ± 9.18)	15, 51–79 (63.40 ± 7.36)	14, 61–84 (66.86 ± 6.14)
ASCT II	10, 27–75 (58.00 ± 13.08)	10, 40–57 (47.60 ± 6.20)	3, 55–56 (55.33 ± 0.58)	40, 59–96 (74.82 ± 8.11)	15, 54–82 (64.40 ± 7.78)	11, 60–88 (68.55 ± 7.06)
ASCT III	11, 20–68 (52.55 ± 12.68)	11, 44–54 (48.73 ± 2.94)	3, 54–58 (55.33 ± 2.31)	35, 59–90 (74.46 ± 7.58)	15, 53–83 (67.73 ± 7.48)	12, 59–83 (70.25 ± 6.61)
ASCT IV	11, 35–74 (62.64 ± 11.07)	11, 42–67 (56.09 ± 7.38)	1, 59	40, 51–99 (83.10 ± 10.20)	15, 59–96 (74.00 ± 9.97)	13, 63–82 (75.15 ± 5.80)
GiLC	19, 20–25 (22.95 ± 1.90)	7, 22–24 (23.29 ± 0.75)	3, 25–26 (25.33 ± 0.58)	100, 20–28 (24.85 ± 1.22)	5, 22–30 (25.20 ± 3.03)	10, 24–26 (24.90 ± 0.88)
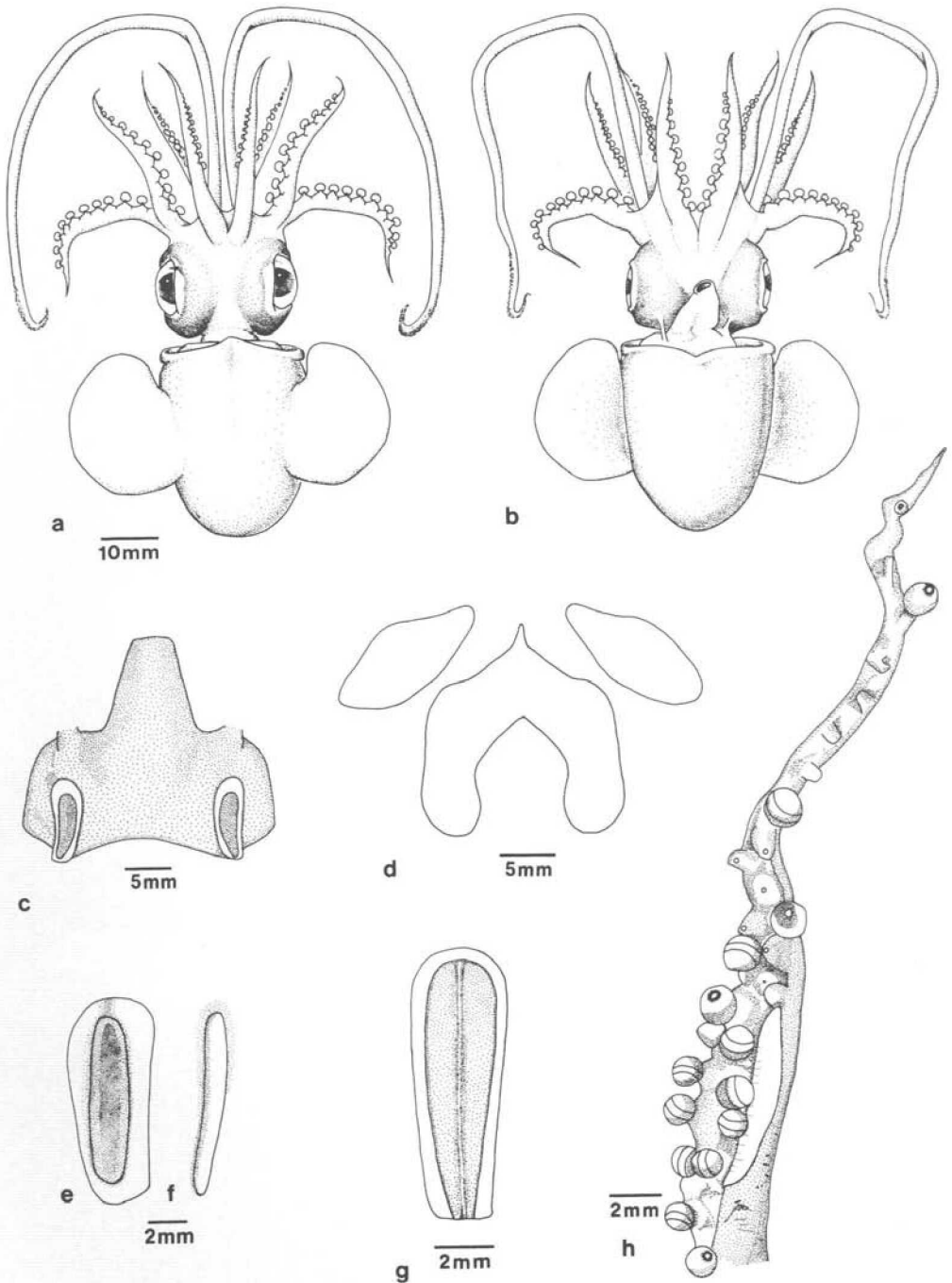
Figure 18. *Rossia* sp. 1 a) dorsal view, male, WAM 970.87, 28.5 mm ML; b) ventral view, WAM 970.87; c) funnel, female, MV F57496, 36.8 mm ML; d) funnel organ, female, MV F57498, 40.0 mm ML; e) funnel locking cartilage, female, MV F57496; f) mantle locking cartilage, female, MV F57496; g) nuchal locking cartilage, female, MV F57496; h) hectocotylus, left Arm I, MV F57496, 29.6 mm ML.

Table 20. Ranges, means and standard deviations of measurements and indices of *Rossia australis* females (203 specimens divided into 5 mm size classes)

Size class (ML mm)	15.0–19.9	20.0–24.9	25.0–29.9	30.0–34.9	35.0–39.9
N, Size, Range ($\bar{x} \pm SD$)	1, 17.6	4, 21.1–23.8 (22.35 ± 1.11)	9, 25.2–29.7 (28.38 ± 1.36)	23, 30.0–34.8 (33.02 ± 1.79)	35, 35.3–39.9 (37.92 ± 1.39)
MWI ($\bar{x} \pm SD$)	72.1	4, 59.2–77.7 (70.66 ± 8.26)	9, 63.6–80.5 (70.25 ± 5.50)	23, 52.1–115.5 (72.05 ± 12.73)	35, 55.7–97.6 (70.84 ± 8.60)
HLI	77.8	4, 54.6–87.9 (71.58 ± 14.22)	9, 54.7–79.9 (67.56 ± 8.97)	23, 56.6–81.4 (68.70 ± 6.14)	34, 49.5–77.6 (65.05 ± 6.68)
HWI	88.1	4, 80.4–102.9 (89.99 ± 10.61)	9, 72.3–96.9 (83.94 ± 8.00)	21, 68.8–90.4 (79.71 ± 5.79)	31, 58.2–97.6 (76.78 ± 9.07)
EDI	57.4	4, 61.8–68.3 (65.25 ± 3.12)	9, 50.4–67.2 (59.26 ± 5.94)	23, 37.6–64.1 (56.58 ± 6.00)	34, 37.3–61.3 (53.87 ± 4.82)
NCLI	25.6	4, 21.9–25.6 (23.34 ± 1.62)	9, 20.2–24.6 (22.80 ± 1.57)	23, 18.7–25.6 (22.27 ± 1.75)	35, 19.7–36.7 (23.36 ± 4.11)
NCWI	6.8	4, 7.1–9.1 (8.16 ± 0.79)	9, 6.7–8.7 (7.56 ± 0.74)	23, 4.4–8.6 (7.51 ± 0.90)	35, 2.8–11.0 (7.36 ± 1.79)
FuLI	42.0	4, 34.6–41.1 (38.34 ± 3.11)	8, 31.2–49.0 (41.48 ± 6.01)	22, 32.2–50.9 (39.47 ± 5.11)	32, 26.8–46.6 (36.55 ± 3.66)
AI I	68.2	2, 98.2–100.0 (98.88 ± 0.94)	7, 85.9–107.9 (94.73 ± 8.21)	21, 77.6–110.6 (91.47 ± 9.50)	31, 66.7–105.4 (86.54 ± 9.45)
ALI II	—	4, 96.6–111.6 (104.1 ± 7.1)	8, 92.5–109.8 (100.9 ± 6.3)	17, 86.2–121.0 (104.5 ± 9.6)	27, 72.6–121.1 (95.9 ± 9.9)
ALI III	92.0	3, 108.6 – 111.6 (109.8 ± 1.6)	8, 93.9–123.7 (107.8 ± 9.6)	18, 86.2–138.2 (108.4 ± 14.1)	29, 81.8–132.9 (103.9 ± 11.8)
ALI IV	68.2	4, 4.8–108.6 (101.7 ± 5.7)	8, 95.2–110.3 (105.1 ± 4.9)	19, 71.2–108.8 (94.95 ± 10.39)	29, 71.8–113.2 (93.90 ± 9.42)
TtLI	—	1, 373.9	4, 306.1–431.5 (372.1 ± 55.6)	6, 297.7–410.9 (342.8 ± 51.5)	22, 193.3–417.6 (323.4 ± 60.4)
ClLI	—	1, 90.3	4, 82.2–105.4 (95.25 ± 10.60)	7, 46.3–105.9 (80.18 ± 18.32)	21, 53.8–102.6 (79.61 ± 13.74)
ASIn I	4.0	4, 4.7–5.9 (5.37 ± 0.56)	4, 4.4–4.6 (4.47 ± 0.07)	9, 2.5–4.8 (4.10 ± 0.84)	18, 3.1–4.8 (3.97 ± 0.47)
ASIn II	5.1	4, 5.7–8.0 (6.68 ± 0.98)	5, 4.8–5.7 (5.34 ± 0.35)	9, 2.5–5.6 (4.64 ± 1.03)	17, 2.6–5.0 (4.43 ± 0.55)
ASIn III	5.1	3, 4.7–6.8 (5.78 ± 1.02)	4, 5.1–5.8 (5.50 ± 0.30)	10, 3.7–6.1 (5.15 ± 0.72)	18, 4.1–6.2 (4.79 ± 0.53)
ASIn IV	4.5	4, 4.7–5.9 (5.25 ± 0.49)	4, 3.8–4.9 (4.39 ± 0.48)	10, 3.4–4.7 (4.06 ± 0.46)	18, 3.1–4.1 (3.70 ± 0.31)
CISI	—	1, 0.42	4, 0.34–0.35 (0.34 ± 0.01)	7, 0.29–0.32 (0.30 ± 0.01)	19, 0.25–0.28 (0.26 ± 0.01)
FPI	10.2	3, 18.5–19.9 (19.05 ± 0.75)	9, 10.3–29.8 (16.73 ± 5.68)	19, 11.5–22.7 (15.93 ± 2.82)	34, 9.3–22.4 (14.79 ± 3.13)
FII	52.3	3, 58.4–63.0 (60.12 ± 2.53)	9, 52.0–66.1 (60.76 ± 4.42)	23, 49.9–71.5 (59.26 ± 4.96)	35, 48.6–67.6 (57.73 ± 4.32)
FLI	67.0	4, 68.7–79.0 (73.76 ± 4.21)	9, 66.1–83.6 (77.51 ± 5.16)	23, 65.0–88.8 (73.97 ± 6.30)	34, 57.1–84.9 (71.99 ± 6.74)
FWSI	48.9	4, 27.6–58.0 (43.18 ± 12.80)	9, 36.0–49.3 (43.74 ± 3.91)	22, 35.6–51.2 (43.71 ± 4.42)	33, 33.2–52.7 (41.64 ± 4.80)
FWTI	136.9	2, 132.7–140.6 (136.7 ± 5.6)	6, 141.2–149.6 (145.9 ± 3.1)	14, 125.0–172.0 (145.8 ± 11.1)	29, 123.1–168.4 (140.4 ± 11.6)
EgDI	— —	— —	— —	13, 6.0–14.1 (10.92 ± 2.27)	28, 6.9–14.6 (10.23 ± 2.10)
NDLI	12.8	4, 13.7–30.3 (24.25 ± 7.44)	9, 25.3–51.4 (33.29 ± 8.51)	23, 24.0–49.0 (40.55 ± 7.31)	35, 32.1–53.3 (42.08 ± 4.52)
NDWI	2.8	4, 3.3–9.9 (6.89 ± 2.72)	9, 7.5–28.8 (15.24 ± 7.16)	23, 5.0–31.6 (20.32 ± 7.23)	34, 16.2–36.3 (24.37 ± 4.46)

Table 20. Continued

| 40.0–44.9	45.0–49.9	50.0–54.9	55.0–59.9	60.0–64.9
72, 40.0–44.7 (42.11 ± 1.42)	43, 45.0–49.7 (47.15 ± 1.31)	12, 50.1–54.9 (52.20 ± 1.50)	5, 55.0–58.4 (56.84 ± 1.40)	1, 62.6
72, 50.2–90.3 (68.32 ± 8.41)	43, 45.5–84.9 (66.06 ± 7.89)	12, 48.7–80.5 (62.65 ± 8.85)	4, 56.7–66.7 (62.33 ± 4.54)	59.1
69, 47.4–82.9 (60.71 ± 7.15)	42, 38.4–81.6 (60.09 ± 7.33)	12, 53.5–73.4 (60.02 ± 6.45)	5, 50.2–69.8 (55.08 ± 8.34)	48.4
64, 55.7–89.9 (72.30 ± 7.19)	41, 58.3–81.0 (67.40 ± 4.93)	11, 58.5–92.9 (68.36 ± 10.17)	2, 65.6–68.1 (66.83 ± 1.76)	59.9
69, 34.4–66.8 (50.74 ± 5.11)	41, 38.7–55.9 (49.38 ± 3.54)	12, 29.5–47.5 (44.21 ± 4.88)	4, 42.2–45.1 (43.61 ± 1.20)	35.1
72, 16.9–34.1 (21.18 ± 2.70)	43, 18.3–32.3 (21.39 ± 2.59)	12, 16.2–23.9 (20.40 ± 2.13)	5, 17.5–22.8 (20.83 ± 2.21)	17.2
72, 2.7–9.5 (7.10 ± 1.09)	42, 3.2–8.5 (6.95 ± 1.10)	12, 4.7–8.2 (6.65 ± 1.00)	5, 6.0–8.2 (6.78 ± 0.87)	6.4
71, 28.1–49.1 (37.35 ± 4.77)	43, 28.0–47.0 (35.37 ± 4.28)	11, 31.8–43.3 (36.99 ± 3.19)	5, 30.4–33.3 (32.29 ± 1.28)	31.5
58, 66.8–106.6 (84.65 ± 9.51)	37, 58.6–114.8 (79.60 ± 10.62)	8, 67.9–95.9 (79.90 ± 9.46)	5, 59.1–94.2 (74.93 ± 12.64)	62.0
60, 68.5–120.0 (95.09 ± 10.07)	34, 72.6–116.5 (87.44 ± 10.34)	9, 75.2–110.5 (89.62 ± 11.06)	3, 80.5–100.2 (88.29 ± 10.45)	80.5
61, 79.6–119.0 (98.27 ± 8.96)	36, 75.5–114.9 (92.25 ± 9.50)	9, 82.7–106.5 (91.03 ± 7.58)	5, 83.6–106.2 (90.31 ± 9.34)	82.3
61, 67.5–118.5 (90.01 ± 8.73)	35, 66.7–114.8 (85.38 ± 10.13)	9, 70.5–92.7 (82.75 ± 7.38)	5, 74.5–95.9 (83.64 ± 8.27)	83.1
45, 205.5–450.2 (302.4 ± 58.5)	27, 203.5–424.6 (288.7 ± 55.7)	8, 196.4–364.3 (300.8 ± 60.6)	2, 196.9–297.9 (247.4 ± 71.5)	147.0
48, 49.4–98.3 (70.56 ± 10.02)	30, 44.6–95.6 (67.43 ± 10.44)	8, 48.9–75.0 (66.89 ± 9.03)	2, 53.5–71.9 (62.73 ± 12.99)	47.9
41, 2.8–4.3 (3.60 ± 0.39)	31, 2.8–3.7 (3.27 ± 0.25)	9, 2.4–3.7 (3.07 ± 0.37)	2, 3.0–3.1 (3.10 ± 0.01)	3.0
39, 3.2–5.5 (4.15 ± 0.46)	29, 3.2–4.5 (3.82 ± 0.32)	7, 2.6–4.5 (3.67 ± 0.59)	2, 3.4–3.5 (3.45 ± 0.0002)	3.8
40, 3.4–5.3 (4.44 ± 0.44)	26, 3.3–4.6 (3.95 ± 0.30)	9, 3.0–4.7 (3.84 ± 0.51)	2, 3.1–3.8 (3.44 ± 0.50)	3.8
41, 3.1–4.2 (3.55 ± 0.27)	28, 2.6–3.5 (3.16 ± 0.23)	7, 2.7–3.3 (3.06 ± 0.21)	2, 2.7–2.9 (2.83 ± 0.15)	2.9
42, 0.22–0.25 (0.24 ± 0.01)	28, 0.20–0.41 (0.22 ± 0.04)	7, 0.18–0.22 (0.19 ± 0.01)	1, 0.17	0.2
70, 9.9–29.5 (16.49 ± 3.61)	42, 10.9–37.2 (16.01 ± 4.73)	11, 10.9–19.4 (15.33 ± 2.30)	5, 12.2–18.3 (15.24 ± 2.22)	18.4
72, 47.2–67.5 (57.13 ± 4.78)	41, 43.4–65.1 (55.28 ± 4.89)	12, 48.1–63.8 (56.76 ± 5.16)	5, 40.7–62.3 (55.49 ± 8.61)	58.3
69, 56.0–86.0 (71.04 ± 7.02)	41, 54.1–77.9 (68.43 ± 5.71)	11, 59.9–75.3 (68.56 ± 5.18)	5, 50.5–72.4 (66.28 ± 8.99)	70.9
71, 28.71–70.1 (40.85 ± 5.92)	42, 25.3–50.8 (39.24 ± 5.09)	11, 30.1–45.8 (38.05 ± 7.45)	5, 33.3–42.7 (33.88 ± 3.91)	41.4
55, 115.5–172.2 (139.1 ± 12.6)	31, 114.9–154.5 (133.9 ± 10.1)	10, 111.3–158.0 (128.7 ± 13.7)	3, 118.1–132.0 (126.5 ± 7.4)	125.9
70, 5.0–14.3 (9.94 ± 1.70)	43, 6.9–11.3 (8.89 ± 1.06)	11, 5.6–10.8 (8.72 ± 1.48)	5, 4.5–8.8 (6.71 ± 1.65)	6.4
72, 30.0–56.9 (43.60 ± 4.84)	43, 20.7–54.9 (43.02 ± 5.79)	12, 36.8–52.8 (45.49 ± 4.45)	5, 42.5–46.9 (44.82 ± 1.90)	39.6
71, 15.3–35.9 (25.77 ± 3.77)	43, 21.6–32.4 (26.83 ± 2.59)	12, 21.0–33.1 (25.63 ± 3.13)	5, 22.0–28.1 (24.68 ± 2.28)	27.1
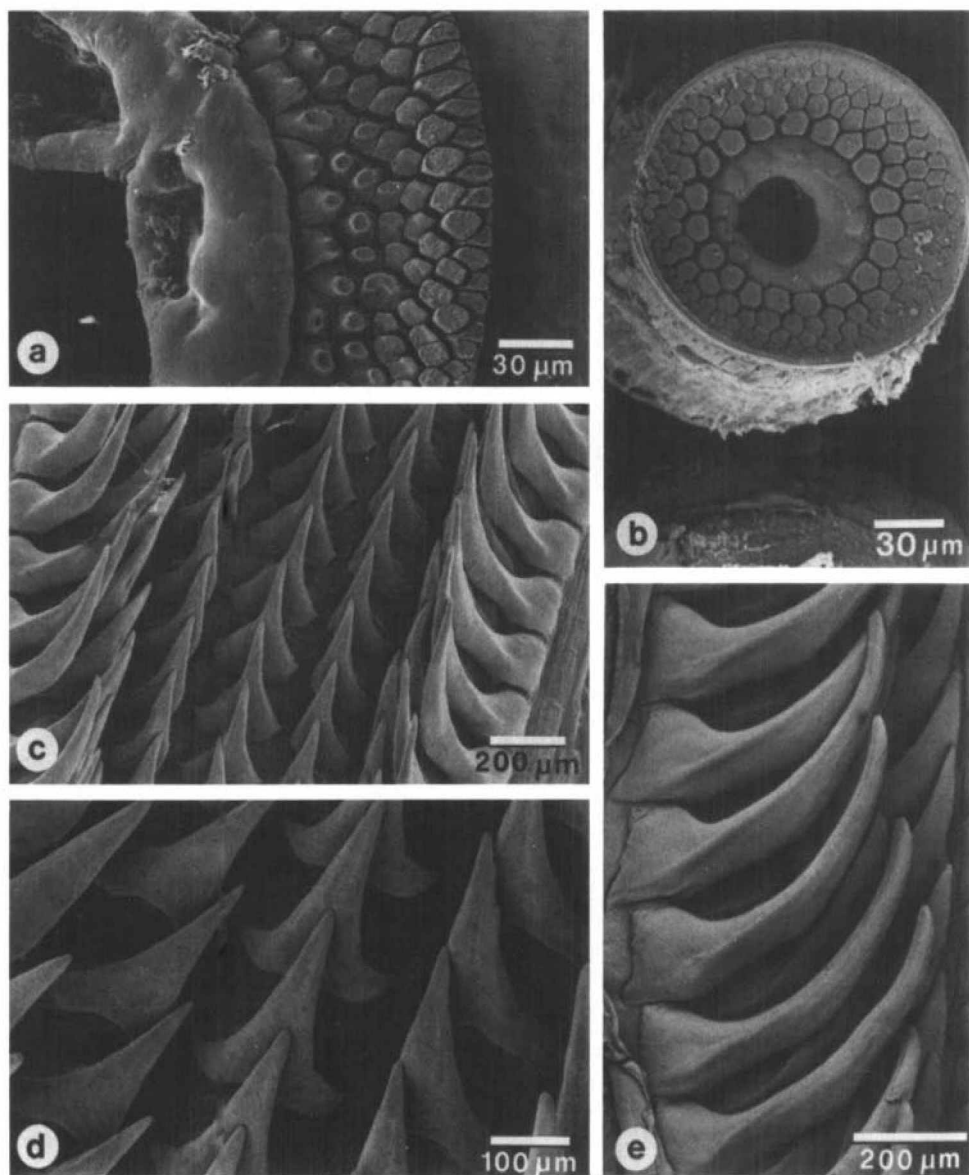
Figure 19. *Rossia* sp. 1 a) Arm sucker rim (arm III), female, WAM 966.87, 51.3 mm ML; b) club sucker, female, MV F57499, 62.9 mm ML; c) radula, female, MV F54923, 46.6 mm ML; d) radula, left to right: 2nd lateral, 1st lateral and rhachidian teeth, female, MV F54923; 3) radula, left to right: 3rd and 2nd lateral teeth, female, MV F57497, 64.6 mm ML.

not be located. This specimen has not been found among Australian Museum collections and has apparently not been located among Berry's private collection (Sweeney et al., 1988).

In addition to the secondary sexual modification of the hectocotylus described above, there were a number of statistically significant morphometric differences between the sexes (Fig. 17). Regression data relating to the features shown in this figure are given in Table 17. With respect to ML, the mantle width, eye diameter
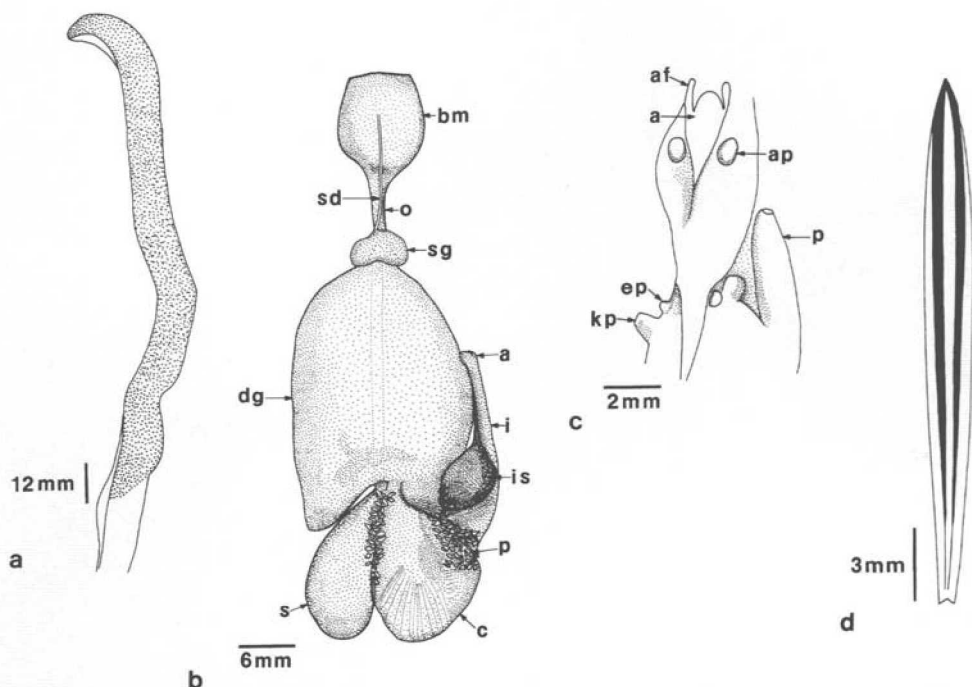
Figure 20. *Rossia* sp. 1 a) left tentacular club, female, MV F57498; b) digestive tract, ventral view, female, MV F57495, 36.6 mm ML, caecum folded back to show connection with stomach and digestive gland (a—anus, bm—buccal mass, c—caecum, dg—digestive gland, i—intestine, is—ink sac, o—oesophagus, p—pancreas, s—stomach, sd—salivary duct, sg—salivary gland); c) portion of anterior mantle organ complex, male, MV F57496, 29.6 mm ML (a—anus, af—anal flap, ap—anal pad, ep—epirenal body, kp—kidney papilla, p—penis); d) gladius, (anterior—top, posterior—bottom), male, MV F54923, 32.8 mm ML.

and nuchal cartilage lengths were greater in females than males of equivalent size range. Funnel length and second, third and fourth arm lengths tended to be greater in males. Tentacle length, club length, fin insertion and total fin width were greater in females. The diameter of the largest sucker on the first dorsal arm was greater in males, reflecting enlargement of hectocotylus suckers. These differences were seen in regression elevations or intercepts. Differences in relative growth rates as reflected by differences in slopes were shown for the first arm length and sucker diameters for arms two, three and four, with males showing faster relative growth rates for these structures than females.

Table 18 compares measurements and indices of *Rossia australis*, *Rossia* sp. 1, and *R. mastigophora* for comparison. Table 19 gives values for meristics. Indices for *Rossia* females divided into 5 mm size classes are given in Table 20.

The preceding analyses support the hypothesis that *Rossia australia* and *R.* sp. 1 are distinct species. The key enable males of each species to be distinguished based upon the range of ratios between two pairs of quantitative characters shown to differ significantly between the two species as shown by ANOVA. However, as previously discussed, no diagnostic qualitative, or single quantitative characters have yet been identified for the two species.

Characters weighting heavily in the formulation of the discriminant function between the two species were for males: AL II, CIL, AS II, AS III and AS IV
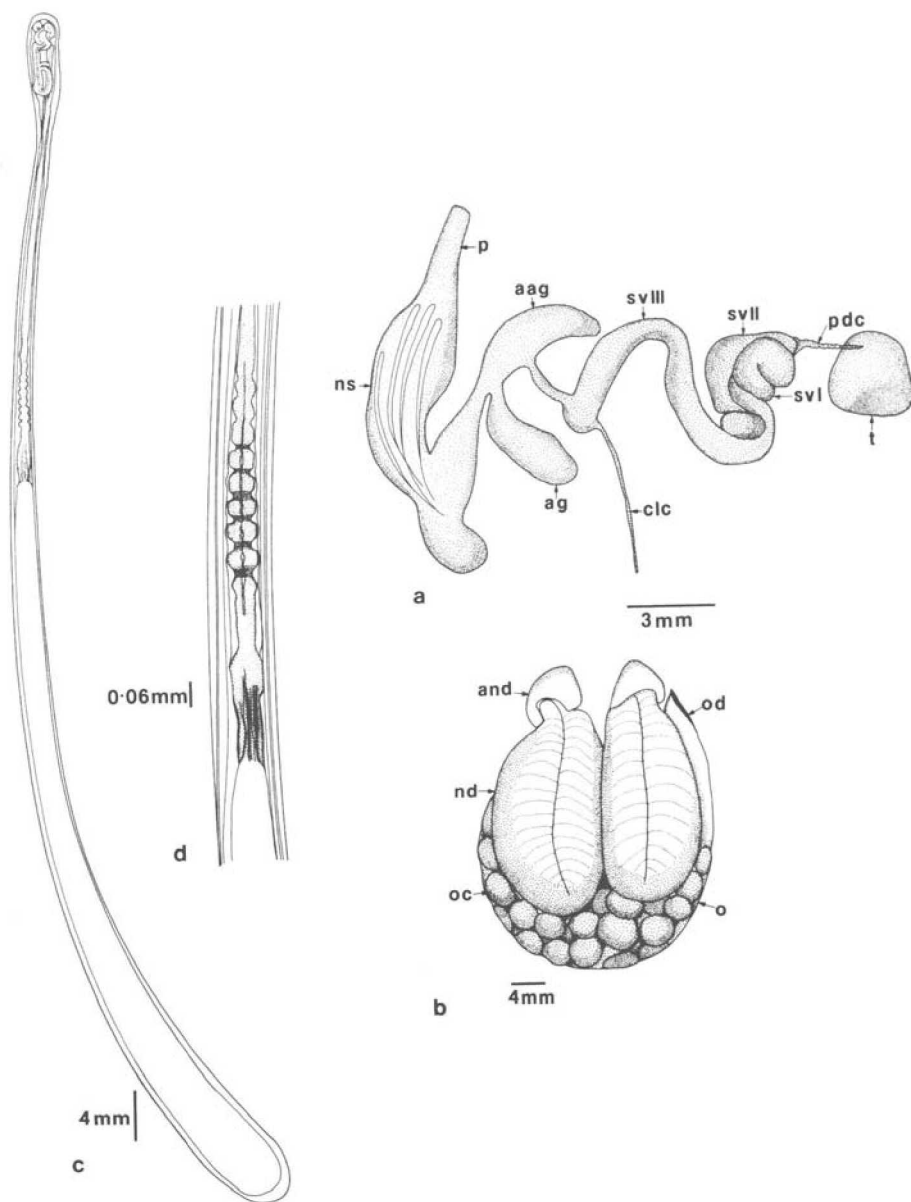
Figure 21. *Rossia* sp. 1 a) male reproductive organs, WAM 970.87, 28.8 mm ML (ag—accessory gland, aag—appendage of accessory gland, clc—ciliated canal, ns—Needhams sac, p—penis, pdc—proximal deferent canal, sv I–III—seminal vesicles I, II, III, t—testis); b) female reproductive organs, ventral view, WAM 971.87, 57.4 mm ML, (and—accessory nidamental gland, nd—nidamental gland, o—ovary, oc—oocyte, od—oviduct); c) whole spermatophore, MV F54923, 34.0 mm ML; d) portion of oral end of spermatophore, base of ejaculatory apparatus connected to sperm reservoir, MV F54923.

(Table 3); and for females: MW, HW and FuL (Table 4), though when examined individually, the range of values for each of these characters overlap considerably. A formula could not be derived to identify females of each species.

Meristic characters showing significant differences were ASCT II for males and ClRC, ASC II and ASCT I–IV for females (Table 5). Of these, though with overlapping ranges, ASCT I, II and IV in females appear to be the most useful
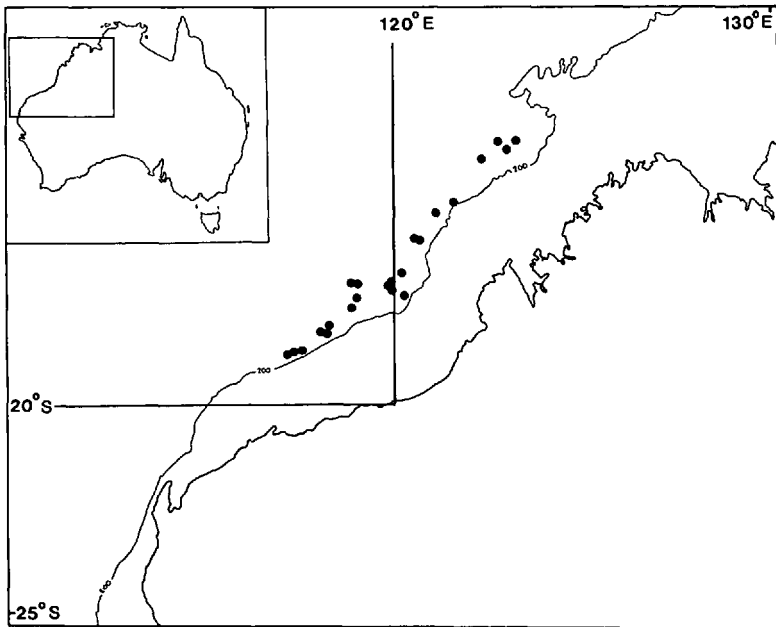
Figure 22. Distribution of *Rossia* sp. 1. Dots indicate collection sites of specimen lots examined in this study.

diagnostically. Remaining characters were shown to covary either with latitude (ClRC and ASC II in females) or longitude (ASCT II in males and ASCT III in females), both when these individual characters for the two species were regressed against geographical position and when *Rossia australis* was examined separately, suggesting caution must be observed when using these characters for diagnostic purposes.

Berry (1918) distinguished *R. australis* from *R. mastigophora* on the basis of the following hectocotylus characters: suckers enlarged on the inner (dorsal) and outer ventral series in *R. australis* (vs. only on the inner series for *R. mastigophora*); only three or four pairs of minute basal suckers in *R. mastigophora* (six or eight pairs in *R. australis*); the apparent lack of lateral pockets in *R. mastigophora* (present in *R. australis*); and the right dorsal arm 4 mm longer than the left in *R. mastigophora*. In Berry's *R. australis* specimens, the right dorsal arms were equal to, or 1–2 mm shorter than the left dorsal arms (table XIV, 256). The club suckers of *R. australis* were described as half the diameter of those of *R. mastigophora*. All of these differences were based on Chun's (1915) description and illustrations. None of these differences were detected between *R. australis* and the African material examined in the present study. However, all suggested differences warrant further investigation. Some of these characters were here observed to be variable in *R. australis*. The glandular web on hectocotylized arms for example, is usually visible, but the glandular part is delicate and may be scraped off during capture. This may explain the absence of the pad in Chun's *R. mastigophora* specimen, or as Chun mentions (p. 313), the specimen he examined was not fully mature and "the transformation of the two dorsal arms which is typical in *Rossia* had not yet taken place." Also, the suckers on the dorsal side of the hectocotylized arms in Chun's illustration do appear to be slightly larger; however, many suckers are missing from the illustrated specimen so this needs to be verified.

Cotton (1938) described and illustrated spermatophores from *R. australis*. The
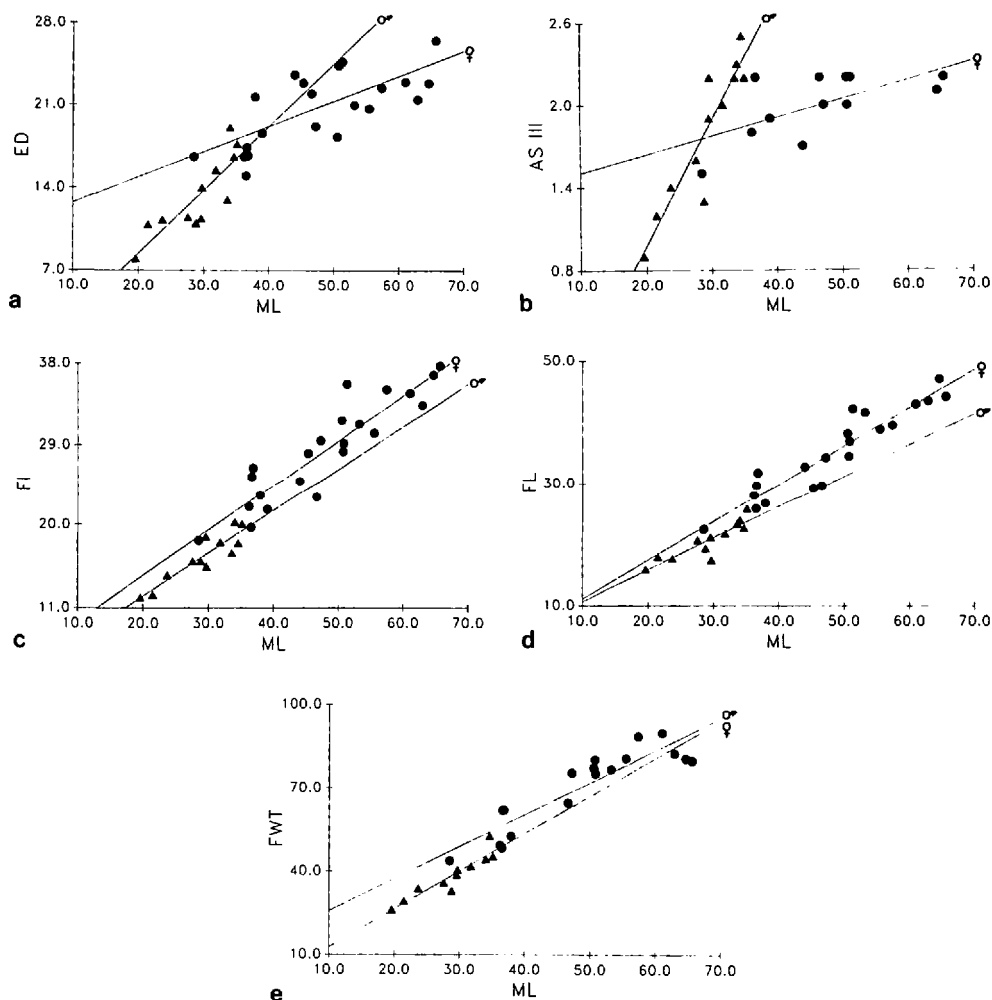
Figure 23.   Sexual dimorphism in *Rossia* sp. 1. For regression formulae and comparison of lines refer to Table 21. Abbreviations for characters are given in Table 1. Solid triangles = males, solid circles = females.

spermatophores bear no resemblance to those examined in this study. The fact that Cotton's specimens were collected at a depth of only 4 feet, makes it extremely unlikely that the specimens were referable to *Rossia*. They are likely to be *Euprymna tasmanica*.

<div align="center">

Rossia sp. 1
Figures 14b, 18–23; Tables 18, 19, 21, 22; Appendix 1b

</div>

Material Examined. — A complete list of material examined is given in Appendix 1b.

Description. — Identical in most qualitative characters to *Rossia australis,* differing slightly in the following respects. Illustrations are included for comparison. Where there are no apparent differences, reference to the figure number only is given.

Fins; FLI: males, 58.25–*71.05*–82.79; females, 63.73–*73.15*–86.41. FWSI: males, 31.25–*41.25*–45.58; females 35.88–*43.77*–55.19 (Fig. 18a, b).

Table 21. Morphological parameters showing sexual dimorphism in *Rossia* sp. 1. Regression data relating to figures where $Y = a + bX$ where Y = dependent variable, a = intercept, b = slope, X = ML, Sig. = significant difference between the regression lines of males (M) and females (F) with respect to slope or intercept (int.); *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant. (Significance of individual regression lines the same in all cases: $P < 0.001$.) r^2 = proportion of total variation accounted for by regression

Y	Sex	N	r^2	a	b	Sig.
ED	M	12	0.719	−2.29	0.536	* (slope)
	F	22	0.500	10.59	0.215	
AS III	M	12	0.850	−0.84	0.091	*** (slope)
	F	12	0.407	1.37	0.013	
FI	M	12	0.828	2.88	0.469	* (int.)
	F	22	0.833	4.53	0.498	
FL	M	12	0.784	5.47	0.515	* (int.)
	F	21	0.881	4.72	0.629	
FWT	M	11	0.858	−0.79	1.359	** (int.)
	F	18	0.819	14.04	1.159	

Funnel; Figure 18c. Funnel valve prominent, ovoid anteriorly. Dorsal funnel organ; Figure 18d. Funnel locking cartilage; Figure 18e. Mantle locking cartilage; Figure 18f.

Head width equal to length in both sexes (mean HW/HL = 100.5%), narrower than mantle in females, usually slightly wider than mantle in males (mean HW/MW: males, 109.7%; females, 92.4%). Eyes; EDI: males, 38.19–*45.56*–56.18; females, 34.18–*44.52*–58.25. Nuchal locking cartilage; Figure 18g, mean NCL/NCW: males, 2.97; females 3.03.

Arm formula usually III:II:IV:I or III:II:I:IV. Indistinct keel present on median aboral sides of arms IV. Suckers not enlarged to extent seen in males (Table 18, Fig. 23b). Arm sucker dentition; Figure 19a. Infundibulum with 6–7 rows of hexagonal processes with blunt pegs. Hectocotylus; Figure 18h. Ventro-lateral edge of oral arm surface bordered by swollen glandular crest, inner edge of which forms a deep furrow extending from sucker rows 4–5 to 8–11 (usually 4–9). Suckers 8–10 rows small, next 3–6 rows enlarged, remaining suckers diminish in size distally.

Tentacle length 1–5 times ML; semicircular in section; oral surface flattened with groove extending to club base. Club; Figure 20a. ClRC: males, 22.0–*24.20*–27.0; females, 33.0–*36.92*–46.0. Club sucker dentition; Figure 19b; inner ring with 8–13 blunt projections.

Beak; Figure 14b. Radula with seven transverse rows of teeth. Rhachidian teeth broad based, without cusps, tapering, fine, diamond shaped with pointed projection toward the base. Base of 3rd laterals flattened with a distinct point posteriorly. Outer face of this tooth usually flattened and pointed posteriorly, a strong ridge developed longitudinally along the middle of the tooth (Fig. 19c, e). Of 4 males (mean ML 29.6 ± 3.3 mm) and 7 females (mean ML 46.0 ± 9.7 mm) examined, mean rhachidian tooth size less in males (mean RL: males, 161.1 ± 37.3 µm; females, 272.3 ± 25.5 µm).

Digestive System (Fig. 20b).—Paired epirenal bodies present in males (Fig. 20c). Gladius; Figure 20d.

Reproductive System.—MALES; Figure 21a. Spermatophores; Figure 21c; SpLI = 17.34–*22.40*–29.41, SpWI = 1.16–*1.47*–1.76. Ejaculatory apparatus; Figure 21d.

Table 22. Selected characters of *Rossia* (*Austrorossia*) species. Abbreviations: M = males, F = females, EP = epirenal bodies, AP = anal pads, P = present, A = absent, GC = glandular crest. * Distalmost and proximalmost suckers larger than remaining median suckers in both sexes. ** Small, paired, ovoid glandular structures which lie midway between the anal opening and kidney papillae occur in both sexes of this species (and in no other *Rossia* examined to date)

Species	Source	Club sucker rows	Epirenal bodies/ anal pads	Hectocotylus suckers Proximal–distal	Distribution
R. australis Berry 1918	Berry, 1918 This study	18–26 M 25–33 F *	P M, A F/P MF	4–9 rows small 4–8 rows enlarged GC rows 4–6 to 8–11	Australia: Raine Isladn (Qld) to Great Australian Bight (W.A.)
R. sp. 1	This study	22–27 M 33–46 F *	P M, A F/P MF	4–9 rows small 3–6 rows enlarged GC rows 4–5 to 8–11	Australia: North West Shelf
R. bipapillata Sasaki 1920	Sasaki, 1920 Saskai, 1929 Voss, 1963	20–40 F *	P M, P F/P MF	?	Japan, Philippines
R. enigmatica Robson 1924	Robson, 1924 Voss, 1962	23–40 MF	P #1 MF	4 rows small 3–4 rows enlarged GC 5–9	Southern Africa
R. mastigophora Chun 1915	Chun, 1915 Boletzky, 1971 This study	23–40 F 30–35 M *	P M, A F/P MF	8 rows small 4 rows enlarged GC 5–11	Southern Africa
R. antillensis Voss 1955	Voss, 1955 Voss, 1956 Boletzky, 1971	30–40 MF	A M, A F/A MF **	6 rows small 6 rows enlarged GC 3–5 to 8–11	Caribbean, Cuba, Dry Tortugas, Western Florida

FEMALES; Figure 21b. Ovary contains oocytes of various sizes, largest round, translucent with mean diameter 8.4 mm.

Color in alcohol cream with pink chromatophores.

Size at Maturity. — ML: males, 19.60–*29.13*–35.10; females, 28.50–*48.10*–65.60. The smallest male in which spermatophores were found was 27.6 mm ML. All females of ML >43 mm ML, NDL >19.6 mm, NDL/NDW 1.33–2.47 contained well developed eggs in the ovary. All material examined was collected from August to February with immature specimens found among the November–February samples. As samples have not been collected right throughout the year, the actual time of reproduction cannot be determined.

Distribution. — Western Australia, North West Shelf from 18°40′S, 117°13′E to 13°25′S, 122°47′E (Fig. 22). Depth 304–455 m.

Remarks. — There are a number of statistically-significant morphometric differences between the sexes. These are shown in Figure 23. Regression data relating to the features shown in this figure are given in Table 21. Relative to mantle length, the length and total width of the fins (reflecting greater mantle width) and length of fin insertion is greater for females than males, although there was no difference in the width of individual fins. Eye diameter and the diameter of the largest sucker on Arm III show different growth rates between the sexes with males showing a faster rate for both these characters as indicated by differences in slopes of regression lines. Table 18 gives ranges, means and standard deviations of measurements and indices of *R. australis, R.* sp. 1, and *R. mastigophora* examined in this study. Table 19 compares meristics.

Distinguishing features of *Rossia (Austrorossia)* nominal species are given in Table 22. Information was derived from descriptions and from examination of specimens of all species. Only those characters in which differences between species could be found (either from published descriptions, or examination of specimens) were included in the table. It can be seen that only *R. bipapillata* (with epirenal bodies in females) can be readily distinguished from the remaining species when individual qualitative characters only are considered (see also Remarks section *Rossia australis*). Appendix 5 lists distinguishing features of *Rossia (Rossia)* for comparison.

Neorossia leptodons new species
Figures 14d, 24–28; Tables 23, 24; Appendix 1d

Material Examined. — A complete list of material examined is given in Appendix 1d.

Type Material. — Holotype; 31 mm male; MV F57504. Paratypes: MV F52341 (28.1 mm ML female); MV F57502 (39.0 mm ML female); MV F57503 (40.0 mm ML female); MV F57505 (14.5 mm ML female); MV F57506 (37.4 mm ML female); MV F57507 (25.7 mm ML female); MV F57514 (41.3 mm ML female); MV F57515 (39.1 mm ML female); MV F57516 (34.5 mm ML female); AM C161456 (57.4 mm ML female); AM C161457 (53.3 mm ML female); AM C161458 (27.9 mm ML male, 52.8 mm ML female); AM C161459 (54.0 mm ML female); AM C161460 (36.1 mm ML male); AM C161461 (77.4 mm ML female); AM C161462 (71.3 mm ML female); AM C161463 (40.0 mm ML male); AM C161464 (53.8 mm ML female); AM C161465 (40.0 mm ML female; with badly damaged male); SAM D18632 (44.9 mm ML female); SAM D18724 (67.6 mm ML female); SAM D18725 (40.3 mm ML male); SAM D18726 (39.6 mm, 41.1 mm and 41.2 mm ML males).

Diagnosis. — Rhachidian and first lateral teeth are relatively narrow, with a truncate to only slightly concave base, tapering distally to a blunt tip.

Description. — Mantle short, broad, cylindrical in anterior half, rounded posteriorly; median antero-dorsal edge of mantle with shallow crescentric emargination,

Table 23. Ranges, means and standard deviations of measurements and indices of *Neorossia leptodons* and *N. caroli* males and females

Index/measure	Males		Females	
	N. leptodons	*N. caroli*	*N. leptodons*	*N. caroli*
ML (N, range)	7, 25.0–41.2	7, 29.4–44.7	16, 14.5–77.4	9, 22.8–82.5
($\bar{x} \pm$ SD)	(35.23 ± 6.92)	(37.01 ± 5.01)	(44.42 ± 16.26)	(45.98 ± 19.65)
MWL	7, 65.6–86.4	7, 66.9–86.4	16, 67.6–92.5	9, 61.2–88.4
	(78.20 ± 7.70)	(76.27 ± 7.54)	(81.77 ± 7.18)	(70.09 ± 8.15)
HLI	7, 66.8–89.6	7, 63.3–77.3	16, 58.4–85.5	9, 50.1–75.3
	(73.81 ± 7.77)	(71.42 ± 4.23)	(71.97 ± 7.87)	(66.99 ± 7.47)
HWI	6, 80.0–111.1	6, 79.4–119.6	16, 67.7–101.4	9, 60.6–100.6
	(91.45 ± 11.57)	(94.66 ± 15.41)	(87.17 ± 9.00)	(84.09 ± 17.30)
EDI	5, 47.2–74.2	7, 52.7–63.9	16, 36.8–57.0	9, 33.7–61.8
	(58.75 ± 9.95)	(57.68 ± 3.34)	(50.04 ± 6.11)	(51.40 ± 10.16)
NCLI	7, 13.2–21.5	7, 19.0–23.7	16, 16.3–23.3	9, 17.3–22.2
	(18.81 ± 3.04)	(21.00 ± 1.58)	(20.07 ± 2.23)	(19.39 ± 1.57)
NCWI	7, 8.0–14.34	7, 8.8–11.6	16, 10.0–15.3	9, 4.7–12.4
	(10.85 ± 2.29)	(10.49 ± 1.09)	(12.37 ± 1.49)	(9.48 ± 2.26)
NCL/NCW	7, 1.5–2.2	7, 2.6–4.4	16, 1.5–1.9	9, 1.7–4.0
	(1.76 ± 0.28)	(3.87 ± 0.67)	(1.63 ± 0.16)	(2.18 ± 0.71)
FuLI	7, 37.4–59.8	7, 42.9–51.6	16, 31.2–86.2	9, 41.0–57.6
	(48.03 ± 7.02)	(46.72 ± 3.42)	(48.56 ± 12.51)	(49.29 ± 5.14)
ALI I	7, 65.6–111.1	7, 72.0–100.9	15, 62.5–105.1	9, 68.0–92.1
	(86.37 ± 17.56)	(85.96 ± 11.42)	(87.80 ± 12.37)	(81.06 ± 8.06)
ALI II	7, 71.2–111.1	7, 87.9–109.6	16, 76.2–107.0	9, 83.3–111.8
	(94.66 ± 16.49)	(99.09 ± 7.95)	(94.90 ± 8.89)	(97.07 ± 10.66)
ALI III	6, 85.0–125.4	6, 86.5–127.0	16, 78.8–120.6	9, 96.5–123.7
	(106.5 ± 13.94)	(110.4 ± 13.8)	(106.7 ± 10.4)	(109.8 ± 9.8)
ALI IV	7, 69.6–107.9	6, 83.6–112.6	16, 74.5–115.0	8, 82.7–111.8
	(93.63 ± 16.26)	(98.76 ± 10.94)	(97.38 ± 12.07)	(99.75 ± 10.32)
TtLI	6, 121.6–365.6	7, 119.0–277.4	15, 110.1–475.9	9, 142.0–400.0
	(210.8 ± 88.26)	(200.7 ± 51.1)	(244.5 ± 95.0)	(233.2 ± 84.2)
ClLI	6, 32.8–82.4	7, 36.0–71.2	15, 48.3–92.5	9, 43.5–78.9
	(53.49 ± 16.40)	(54.72 ± 12.74)	(65.21 ± 13.23)	(61.64 ± 13.91)
ASIn I	7, 3.6–5.7	6, 3.4–4.9	16, 2.8–5.1	9, 2.3–4.7
	(4.15 ± 0.75)	(4.08 ± 0.61)	(3.92 ± 0.62)	(3.51 ± 0.85)
ASIn II	7, 4.0–7.9	6, 4.8–5.6	16, 3.5–5.8	9, 2.7–5.4
	(5.71 ± 1.20)	(5.29 ± 0.31)	(4.57 ± 0.68)	(3.93 ± 0.94)
ASIn III	7, 4.8–7.5	6, 4.7–6.1	16, 3.5–6.2	9, 3.0–5.8
	(6.07 ± 1.03)	(5.38 ± 0.46)	(4.70 ± 0.81)	(4.18 ± 1.01)
ASIn IV	7, 4.0–6.4	6, 4.3–5.3	16, 2.8–5.2	9, 1.7–4.8
	(5.23 ± 0.81)	(4.83 ± 0.41)	(3.90 ± 0.63)	(3.55 ± 0.97)
CISI	6, 0.72–1.79	6, 0.67–1.02	15, 0.80–1.42	9, 0.46–1.21
	(1.03 ± 0.42)	(0.83 ± 0.12)	(1.04 ± 0.16)	(0.84 ± 0.27)
FPI	6, 15.2–27.3	7, 14.2–20.1	16, 9.4–26.2	9, 12.4–24.2
	(20.18 ± 4.77)	(17.65 ± 2.22)	(17.72 ± 4.37)	(17.22 ± 3.43)
FII	6, 50.8–69.5	7, 44.9–62.4	16, 41.4–74.9	9, 53.7–70.9
	(63.17 ± 6.98)	(54.39 ± 6.83)	(62.22 ± 7.77)	(59.42 ± 7.05)
FLI	5, 48.4–86.0	6, 54.0–78.9	16, 49.0–92.2	9, 57.0–89.1
	(68.73 ± 16.22)	(64.08 ± 9.64)	(73.19 ± 10.82)	(72.14 ± 10.71)
FWSI	6, 36.0–50.8	6, 31.8–47.6	16, 31.8–58.5	8, 26.9–48.9
	(41.86 ± 5.46)	(39.10 ± 6.19)	(42.71 ± 8.34)	(39.67 ± 67.73)
FWTI	5, 122.0–172.1	6, 120.2–156.8	16, 87.6–200.0	8, 125.1–163.9
	(153.0 ± 18.9)	(136.8 ± 15.8)	(154.1 ± 25.0)	(138.2 ± 14.5)
FL/FWS	5, 1.2–1.8	6, 1.3–1.9	16, 1.2–2.5	8, 1.4–2.6
	(1.59 ± 0.24)	(1.65 ± 0.20)	(1.76 ± 0.35)	(1.80 ± 0.37)

Table 23. Continued

Index/measure	Males		Females	
	N. leptodons	*N. caroli*	*N. leptodons*	*N. caroli*
EgDI			6, 9.0–17.6 (11.71 ± 3.10)	3, 8.7–11.5 (9.90 ± 1.43)
NDLI			15, 16.4–44.6 (35.74 ± 8.19)	9, 10.1–42.2 (28.41 ± 12.38)
NDWI			15, 5.7–29.4 (17.59 ± 7.10)	9, 3.1–26.5 (12.97 ± 8.80)
SpLI	5, 26.8–41.2 (32.93 ± 6.02)	5, 32.1–47.1 (41.33 ± 5.75)		
SpWI	5, 1.94–2.23 (2.10 ± 0.14)	5, 1.3–2.6 (1.95 ± 0.46)		

without distinct lobes. Antero-ventral mantle edge slightly concave (Fig. 24a, b). Fins large (FLI: males, 48.39–*68.73*–86.03; females, 48.97–*73.19*–92.22. FWSI: males, 36.00–*41.86*–50.79; females, 31.79–*42.71*–58.52) and ovate, attached dorso-laterally within posterior four-fifths of mantle; posterior margins curved, continuous and united around apex of mantle; anterior margins convex with well developed lobes, slightly indented at point of fin insertion, lateral lobes broadly rounded. Anterior edge of fins extend approximately to the level of mantle opening. Funnel conical and broad-based, projecting anteriorly approximately to level of anterior quarter of eye, free for most of its length (Fig. 24c). Funnel valve well developed, rounded. Dorsal funnel organ large, median limbs with broad, blunt lobes, tapered posteriorly and V-shaped anteriorly; single terminal apical papilla

Table 24. Ranges, means and standard deviations of meristic variables for *Neorossia leptodons* and *N. caroli* males and females

| Count	Males		Females	
	N. leptodons	*N. caroli*	*N. leptodons*	*N. caroli*
ClRC (N, range) (x̄ ± SD)	6, 8–10 (9.67 ± 0.82)	7, 9–11 (9.71 ± 0.75)	15, 9–10 (9.93 ± 0.26)	9, 8–10 (9.67 ± 0.71)
ASC I	7, 16–23 (19.14 ± 3.08)	7, 18–24 (20.14 ± 1.86)	16, 15–25 (20.19 ± 2.64)	9, 17–23 (19.56 ± 1.81)
ASC II	7, 15–20 (17.57 ± 1.72)	7, 16–21 (18.43 ± 1.51)	16, 14–24 (19.31 ± 2.39)	9, 19–25 (21.33 ± 2.06)
ASC III	7, 16–22 (19.00 ± 2.16)	7, 18–22 (19.71 ± 1.50)	16, 17–25 (21.19 ± 2.64)	9, 20–27 (23.33 ± 2.29)
ASC IV	7, 16–23 (19.43 ± 2.37)	7, 18–23 (20.14 ± 1.95)	16, 15–25 (21.81 ± 2.71)	9, 20–27 (23.00 ± 2.24)
ASCT I	7, 42–61 (50.57 ± 5.88)	7, 48–57 (51.86 ± 3.53)	16, 34–60 (51.62 ± 6.32)	9, 52–63 (56.33 ± 3.46)
ASCT II	7, 44–60 (52.14 ± 7.62)	7, 44–51 (48.29 ± 3.15)	16, 32–64 (57.12 ± 7.93)	9, 55–67 (62.33 ± 4.21)
ASCT III	7, 44–66 (57.57 ± 5.41)	6, 50–56 (53.33 ± 2.66)	16, 41–68 (59.8 1 ± 6.49)	9, 61–77 (69.67 ± 4.82)
ASCT IV	7, 47–63 (57.75 ± 7.36)	6, 50–70 (58.67 ± 6.74)	16, 38–71 (61.62 ± 7.87)	9, 62–74 (69.56 ± 3.57)
GiLC	6, 20–21 (20.17 ± 0.41)	7, 16–21 (18.86 ± 2.03)	15, 18–21 (19.60 ± 0.83)	7, 17–23 (20.14 ± 2.27)
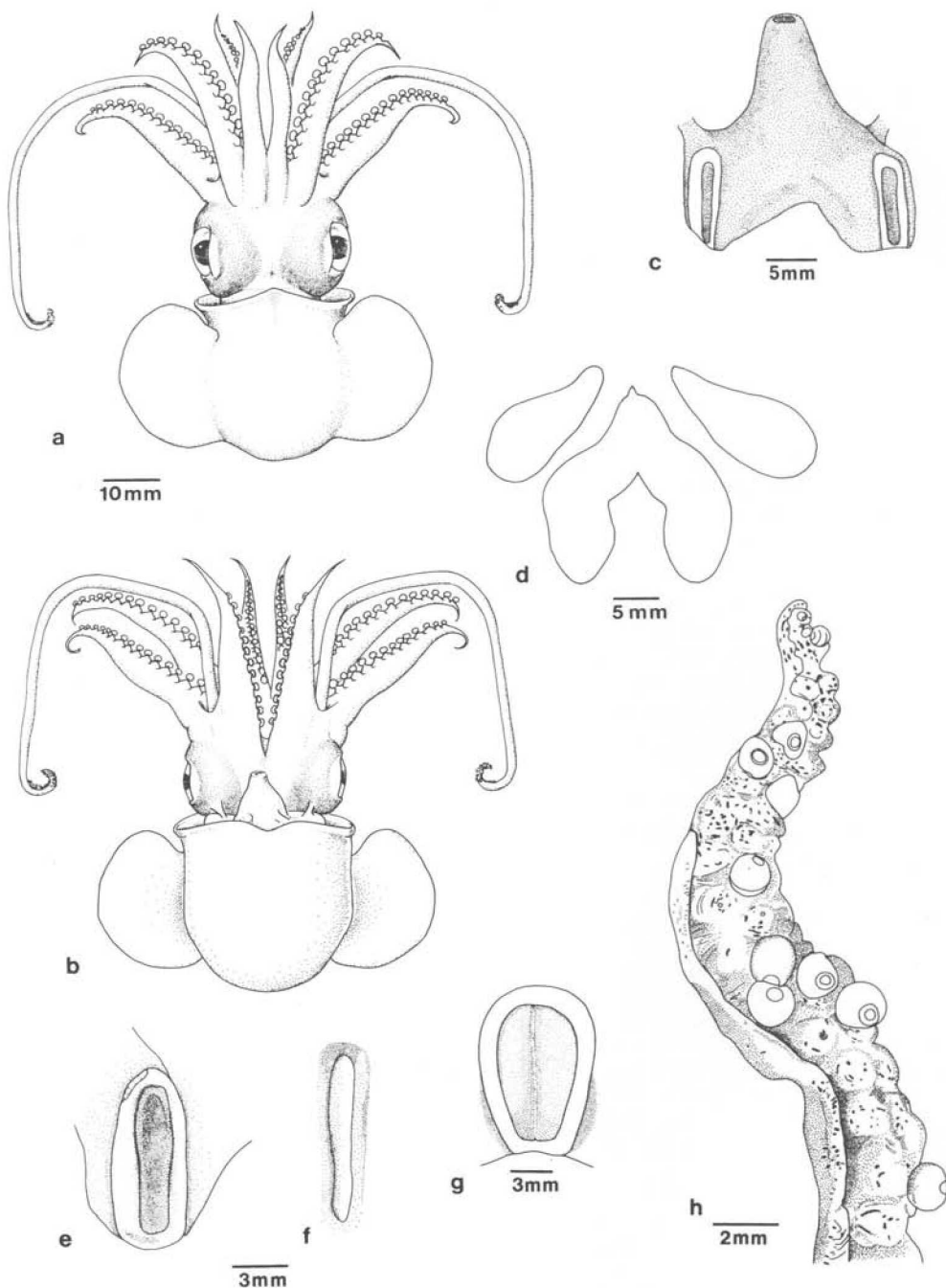
Figure 24.   *Neorossia leptodons* n. sp. a) dorsal view, holotype, male, MV F57504, 31.5 mm ML; b) ventral view, holotype; c) funnel, paratype, female, MV F57514, 39.1 mm ML; d) funnel organ, holotype; e) funnel locking cartilage, paratype, female, MV F52341, 28.1 mm ML; f) mantle locking cartilage, paratype, female, MV F52341; g) nuchal locking cartilage, holotype; h) hectocotylus, right Arm I, holotype.
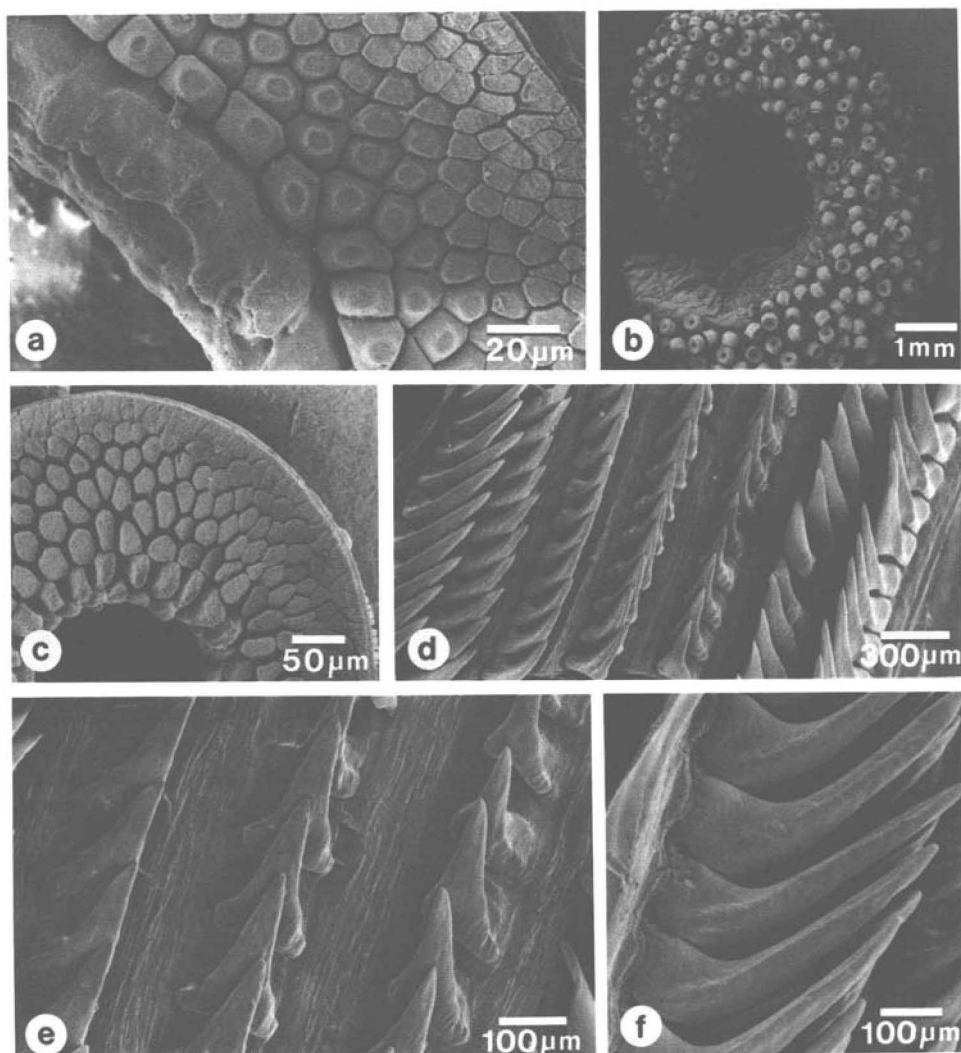
Figure 25. *Neorossia leptodons* n. sp. a) arm sucker rim (Arm III), paratype, female, AM C161457, 53.3 mm ML; b) club, distalmost end, paratype, female, MV F57514, 41.3 mm ML; c) club sucker rim, paratype, male, AM C161458, 27.9 mm ML; d) radula, paratype, female, AM C161458, 52.8 mm ML; e) radula, left to right: 1st lateral and rhachidian teeth, female, AM C161458; f) radula, 3rd lateral teeth, paratype, female, AM C161456, 57.4 mm ML.

simple, narrow pointed; ventral pads ovoid, broader posteriorly, medial borders straight or slightly concave, lateral borders curved (Fig. 24d). Funnel locking cartilage a deep straight groove, the cartilage margin flattened forming a broad rim (Fig. 24e). Mantle locking cartilage a straight narrow ridge (Fig. 24f).

Head broader than long (mean HW/HL: males, 120%; females, 125%), equal to or slightly wider than mantle (mean HW/MW: males, 113%; females, 110%), with slight median depression dorsally and ventrally. Eyes very large and bulbous (EDI: males, 47.20–*58.75*–74.19; females, 36.81–*50.04*–57.00); ventral eyelids free, a small oval olfactory pore present ventro-laterally on posterior surface of
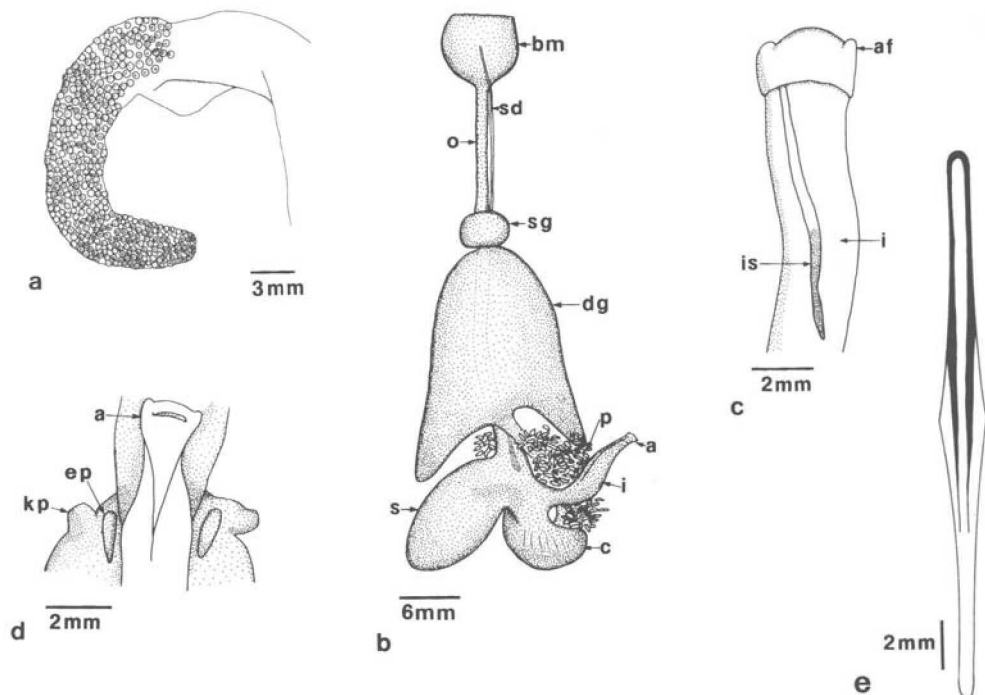
Figure 26. *Neorossia leptodons* n. sp. a) right tentacular club, holotype, male, MV F57504, 31.5 mm ML; b) digestive tract, ventral view, paratype, female, AM C161457, 53.3 mm ML, caecum folded back to show connection with stomach and digestive gland (a—anus, bm—buccal mass, c—caecum, dg—digestive gland, i—intestine, o—esophagus, p—pancreas, s—stomach, sd—salivary duct, sg—salivary gland); c) terminal end of intestine, female, MV unreg., 60 mm ML (af—anal flap, i—intestine, is—ink sac vestige); d) portion of anterior mantle organ complex, paratype, male, AM C161458, 27.9 mm ML (a—anus, ep—epirenal body, kp—kidney papilla); e) gladius (anterior—top, posterior—bottom), paratype, female, MV F57502, 39.0 mm ML.

the eye in a position in line with insertion of third arm. Nuchal locking cartilage (Fig. 24g) broad and ovoid, becoming slightly narrower posteriorly, with wide outer rim and distinct median furrow (NCL/NCW: males, 1.47–*1.76*–2.20; females, 1.50–*1.63*–1.90).

Arms short, robust and broad at bases; order III, IV, II, I (or, frequently III, II, IV, I) in both males and females. All arms similar in shape, semicircular in section. Arms three and four with indistinct keel. Trabeculae on all arms poorly developed, present as small bilobed tubercles arranged on the external face of short pedicles forming a scalloped protective membrane. Arm suckers biserial throughout, spherical; suckers of arms II and III slightly larger in both sexes than arms I–IV (Table 23). Arm sucker dentition (Fig. 25a). Chitinous rings of all arm suckers with inner ring surface almost smooth, margin only very slightly scalloped around entire surface. Infundibulum with 6–7 rows of polygonal processes, inner 3–4 rows each with blunt pegs. At periphery of sucker, processes without pegs arranged radially. From periphery to inner ring, pegs almost equal in size to that of their base, their profile shallow and sometimes irregular. Inner well-developed pegs approximately ½–⅓ diameter of polygonal base. Upper peg surface slightly concave. Hectocotylus. Dorsal pair of arms of males hectocotylized (Fig. 24h). Proximal-most ventral edge of arms on oral surface bordered by a furrow and
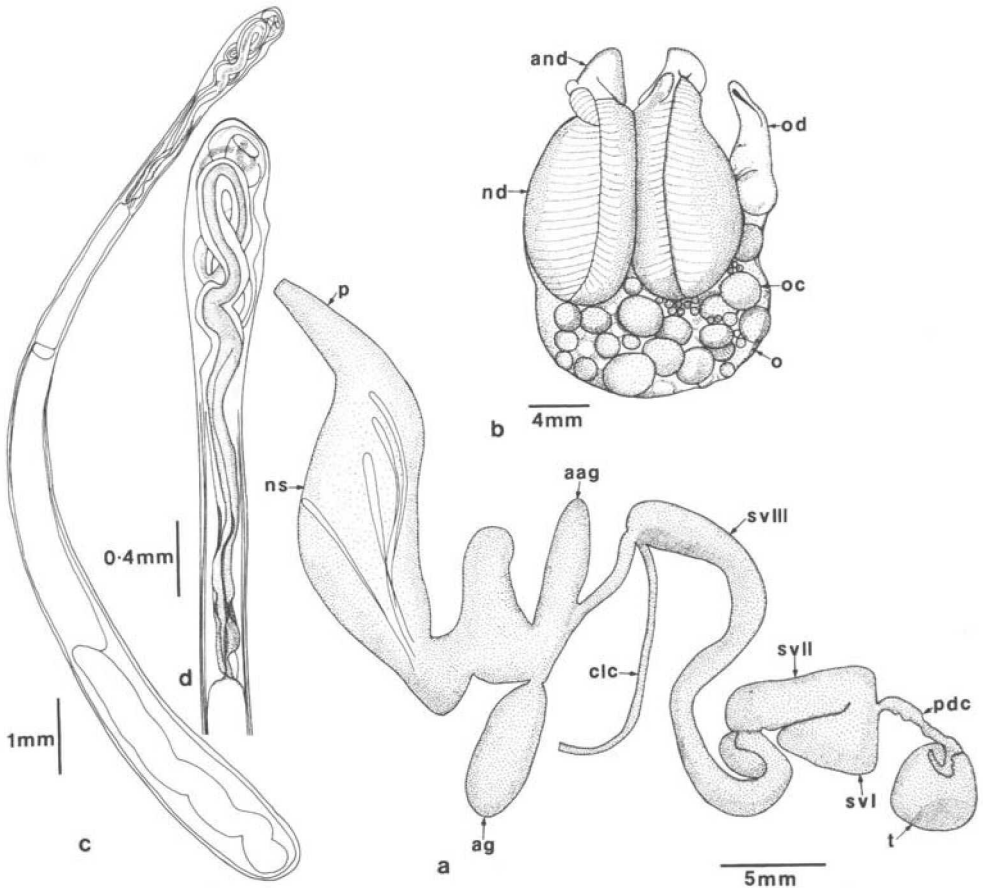
Figure 27. *Neorossia leptodons* n. sp. a) male reproductive organs, paratype, AM C161458, 27.9 mm ML (ag—accessory gland, aag—appendage of accessory gland, clc—ciliated canal, ns—Needhams sac; p—penis; pdc—proximal deferent canal; sv I-III—seminal vesicles I, II, III; t—testis); b) female reproductive organs, ventral view, paratype, AM C161464, 45 mm ML (and—accessory nidamental gland, nd—nidamental gland, o—ovary, oc—oocyte, od—oviduct); c) whole spermatophore, holotype; d) portion of spermatophore, oral end to sperm reservoir, paratype, AM C161458.

crest extending from sucker rows 4–14. Inside crest fleshy with transverse grooves between bases of pedicles and longitudinal crest. Sucker bearing surface of hectocotylized arms broad. Proximal-most dorsal arm border without ridge developed. Suckers of hectocotylized arms smaller than remaining arm suckers.

Tentacles relatively long and slender with naked stalks, length ranging from approximately 2–5 times ML; semicircular in section; flattened oral surface with groove that extends to base of club. Club tapers to tip; curved and slightly expanded with narrow protective membranes (Figs. 25b, 26a). Suckers in 9–10 oblique rows. Distinctive crescentic swimming keel on aboral side of carpus, widest at base of club and extending to approximately 8th sucker row where it terminates abruptly. Club sucker dentition (Fig. 25c). Inner ring narrow with blunt projections. Infundibulum with 6–7 rings of polygonal processes without pegs. Ring of polygonal process slightly raised. At periphery, polygonal processes smaller and elongate. Buccal membranes. With 6 lappets, without suckers. Buccal connectives extend
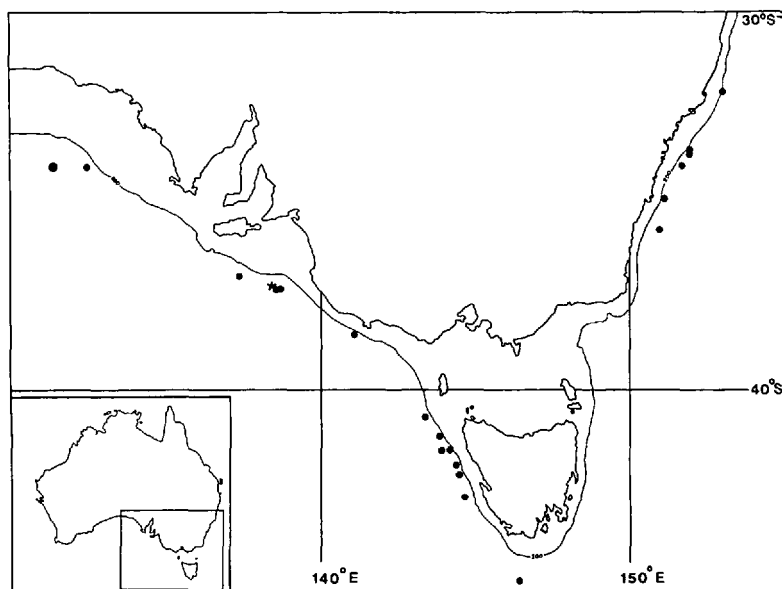
Figure 28.   Distribution of *Neorossia leptodons* n. sp. Dots indicate collection sites of specimen lots examined in this study, * indicates type locality.

approximately to level of first sucker row. Beak. Upper beak with slightly curved rostral edge. Indentation at lateral wall edge shallow. Crest wide. Lower beak with slightly curved rostral edge, crest with pronounced curve. Lateral wall edge not indented. Hood notch absent. Wings widely spread, crest wide. Rostrum produced forwards a little. Jaw angles widely apart. Wing fold to side of jaw angle very low, rounded and slightly thickened. Jaw angle distinct, obtuse. Lateral walls smooth. Chitin of upper and lower beaks black, darkening gradually from rostrum to hood and lateral walls (Fig. 14d). Radula with seven transverse rows of teeth (Fig. 25d–f); rhachidian teeth broader at base, stout and triangular without cusps, the base truncate to slightly concave; first lateral teeth subtriangular, taper gradually to tip. Second and third lateral teeth slender and tapered 1½ to twice as long as median teeth, asymmetrical, displaced toward midline. Of 2 males (mean ML 34.9 ± 1.6 mm) and 6 females (mean ML 51.3 ± 14.8 mm) the average rhachidian tooth size was smaller in males (mean RL: males, 211.0 ± 15.6 μm; females, 274.8 ± 41.9 μm).

Digestive System (Fig. 26b).—Single posterior salivary gland; broad, semicircular, tapering anteriorly with a single salivary duct running forward alongside esophagus entering posteroventral surface of buccal mass in the mid-ventral line. Esophagus runs dorsally along midline of digestive gland, broadening as it enters stomach immediately below posterior end of digestive gland. Stomach a large globose sac, thin posteriorly and with broad muscular band anteriorly encircling stomach transversely. Caecum circular in outline; disc-like, narrow, grooved in a blunt V anteriorly, surface lining finely pleated. A single duct connects digestive gland near the midline with stomach and caecum. Digestive gland large, globular, divided posteriorly into two large subtriangular lobes. Intestine short, wide and undifferentiated. Ink sac reduced to a narrow vestige, attached dorsally to intestine and opening into it via a short, narrow duct just behind the anal opening on the dorsal side. No ink in sac (Fig. 26c). Intestine lies superficially in a groove on

ventral face of the digestive gland. Digestive gland duct with branching, attached pancreatic tissue throughout. Anus with reduced anal flaps (Fig. 26c, d). In males paired epirenal bodies present, lie proximal and slightly anterior to kidney papillae (Fig. 26d).

Gladius. The gladius is visible through integument in the anterior third of mantle then submerges below muscles of the mantle and fins posteriorly. Gladius length approximately 70% ML. Rachis extends posteriorly approximately ⅔ the length of vane, equal width throughout most of its length, tapering in the posterior ⅔. Vane extends from middle part of gladius, broad, diamond shaped anteriorly, wider than gladius (variable, wider in larger specimens), tapering posteriorly to two fine points. Edges of the vane thickened, often sclerotized along the posterior edges (Fig. 26e).

Reproductive System. — MALE (Fig. 27a). Testis on left posterior side of viscero pericardial coelom in close proximity and ventral to caecum. At distal end, convoluted proximal deferent canal opens into a lobe shaped seminal vesicle I. This is connected with seminal vesicle II, composed of a cylindrical part with a rounded appendage. Seminal vesicle III long, S-shaped, joins a delicate ciliated canal (which opens into genital sac) and a narrow tube which connects accessory gland and accessory gland appendage. Accessory gland appendage joins posterior end of Needhams sac via the distal deferent canal. Posterior end of Needhams sac is produced into two large tongue-shaped lobes. Needhams sac large, leaf shaped. Genital orifice opens into anterior end of mantle cavity. Spermatophores (Fig. 27c, d) large (SpLI = 26.76–*32.93*–41.22) sperm mass comprises 71% of length. Aboral end of spermatophore widest, with sperm reservoir approximately equal width throughout most of its length, tapering slightly where connective attaches. Structure of ejaculatory apparatus simple, connected to sperm reservoir by a narrow, cap-shaped cement body. Middle tunic of ejaculatory apparatus narrow, slightly convoluted at the base where it joins the cement body, finely coiled along its length. Oral end of spermatophore dilated enclosing remainder of loosely coiled ejaculatory apparatus. Entire sperm reservoir and ejaculatory apparatus surrounded by a double membrane. FEMALES. Ovary large, occupies large proportion of posterior end of mantle cavity, displacing other organs when mature. Contains oocytes of various sizes, largest round, translucent with mean diameter 11.7 mm. Opens via single thick-walled oviduct at anterior end on the left side. Opening of oviduct modified as a seminal receptacle, often with spermatophores embedded on inner edge of opening to oviduct, giving a granular appearance. Paired tear shaped nidamental glands occupy a position ventral to ovary toward anterior end. Inverted U-shaped accessory nidamental glands are located toward distal end of nidamental glands (Fig. 27b).

Color in alcohol cream with small pink to maroon chromatophores distributed evenly over mantle, fins, head and arms; chromatophores on dorsal surface of mantle, fins and head slightly darker and more concentrated than those on ventral surface. Ventral surface of head devoid of chromatophores in a crescentic arc bordering region of projection of funnel. The funnel in some individuals is evenly scattered with chromatophores, while in others the chromatophores are confined to a midventral patch.

Size at Maturity. — Smallest male in which spermatophores were found was 27.9 mm ML. All females larger than 54 mm ML, NDL > 22.80, NDL/NDW 1.48–2.02 were mature with well developed eggs in the ovary. Two specimens, MV F57506 and AM C161458 with ML 37.40 and 52.8 contained eggs at various stages of development. The largest female was 77.4 mm ML. Thus, males mature

at smaller sizes than females, while the latter attain a much larger size. Large mature specimens have a thick, gelatinous consistency. Mature specimens were collected from August–January in 731–1,098 m. Immature specimens were collected from January–August between 130–1,100 m. No mature specimens have been collected in water shallower than 730 m. Insufficient material precludes definitive conclusions to be drawn, however there is some evidence to suggest that egg laying may occur in deeper waters during spring–summer, followed by migration of juveniles to shallower water.

Type Locality.—South Australia, Great Australian Bight 37°18.81′S, 138°36.3′E–37°17.76′S, 138°35.01′E, 130–1,110 m.

Distribution.—Australia: New South Wales 32°08′S, 153°07′E–South Australia 33°58′S, 131°22′E (Fig. 28). Depth 130–1,110 m.

Etymology.—The specific name is from the Greek *leptos,* narrow or slender, and *odons,* tooth with reference to the teeth of the radula. To be treated as a noun in apposition.

Remarks.—A redescription of *N. caroli* follows to enable comparisons to be made with the present species. Included here are tables comparing morphometric data; Table 23 gives measurements and indices for *N. leptodons* n. sp. and *N. caroli* and Table 24 gives meristics. As previously discussed, this species differs from *N. caroli* in the shape of the radular teeth (Figs. 25d–f, 30c–f, 31). Comparison between Figure 27d and Figure 33d suggests there may be some differences in spermatophore structure. However, these differences are within the variation found within the two species; the base of the ejaculatory apparatus appears to be more tightly compacted in the *N. caroli* holotype than in the *N. leptodons* holotype.

Also, from the illustrations, the swimming keel on the tentacular club of *N. leptodons* n. sp. (Fig. 26a) is wider than that of the *N. caroli* specimen illustrated (Fig. 32a), however, this is not a useful diagnostic character as the width of the keel was found to be quite variable in both species.

One female specimen (AM C161459) was found to have spermatophores embedded in the ventral anterior edge of the mantle.

Redescription of *Neorossia caroli* (Joubin)
Figures 14, 29–34; Tables 23, 24; Appendix 1e

Rossia caroli Joubin, 1902: 138–143, figs. 1, 2. Mangold-Wirz, 1963: 205–224, figs. 1–4, tables I–VI.
Neorossia caroli Boletzky, 1971: 964–969, fig. 1. **Holotype.** Male, 37.4 mm ML, MOM 29-5136.

Diagnosis.—Differs from its congener, *Neorossia leptodons,* in the shape of the radula teeth. Rhachidian and first lateral teeth broad, base usually strongly indented.

Material examined.— A complete list of material examined, including the holotype is given in Appendix 1e.

Description.— Similar in most respects to *N. leptodons* n. sp. Any differences and reference to figures only are given here. Median antero-dorsal edge of mantle with low V-shaped projection. Antero-ventral edge of mantle with shallow crescentic emargination (Fig. 29a, b). Dorsal edge of mantle margin projects beyond ventral mantle edge. Fins; FLI: males, 54.01–*64.08*–78.91; females, 57.01–*72.14*–89.12. FWSI: males, 31.77–*39.10*–47.62; females, 26.89–*39.67*–48.95.

Funnel (Fig. 29c) projects anteriorly approximately to level of anterior half of
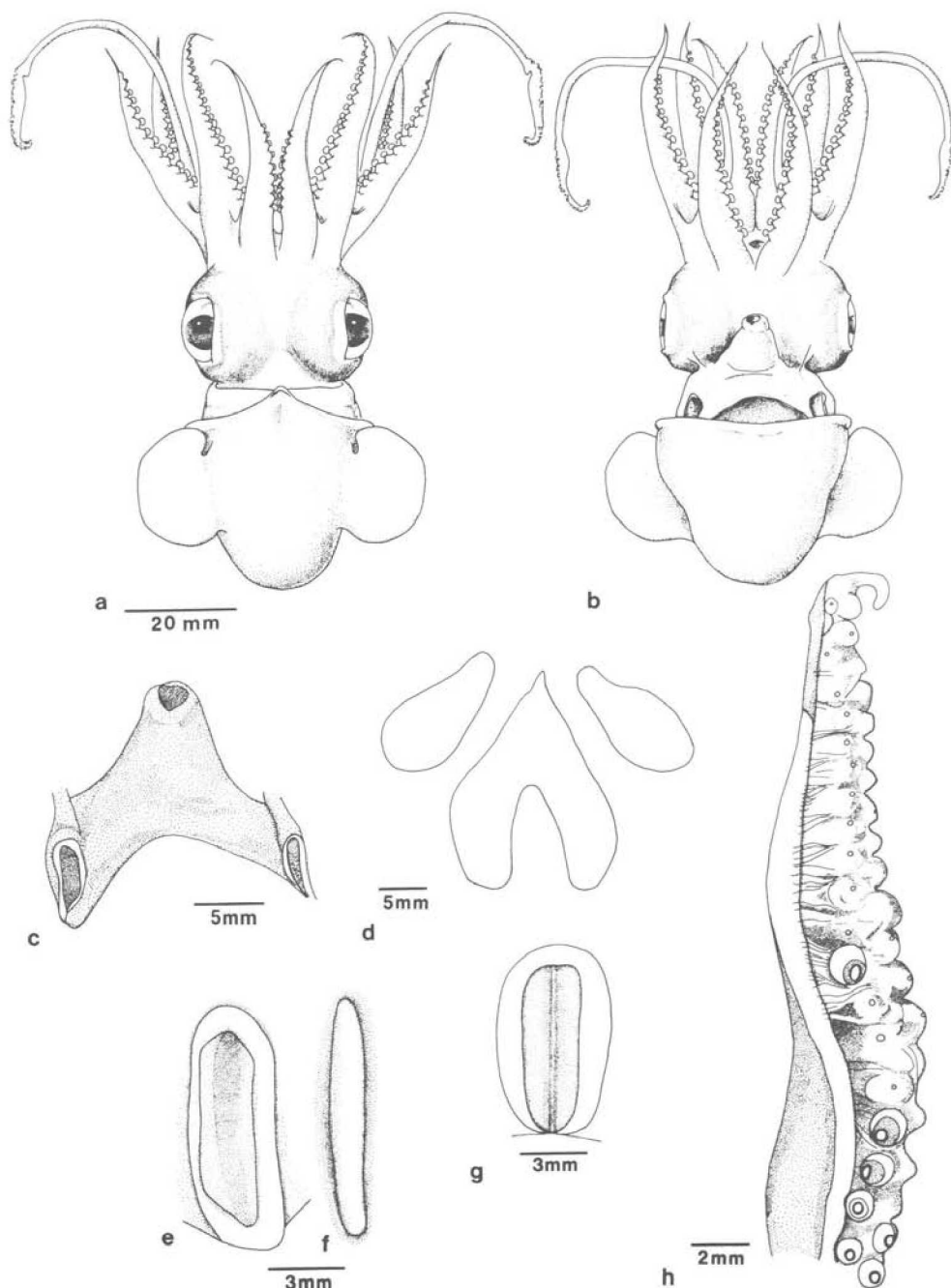
Figure 29. *Neorossia caroli* a) dorsal view, holotype, male, MOM 29-5136, 37.4 mm ML; b) ventral view, holotype; c) funnel, holotype; d) funnel organ, holotype; e) funnel locking cartilage, holotype; f) mantle locking cartilage, holotype; g) nuchal locking cartilage, holotype; h) hectocotylus, right Arm I, holotype.
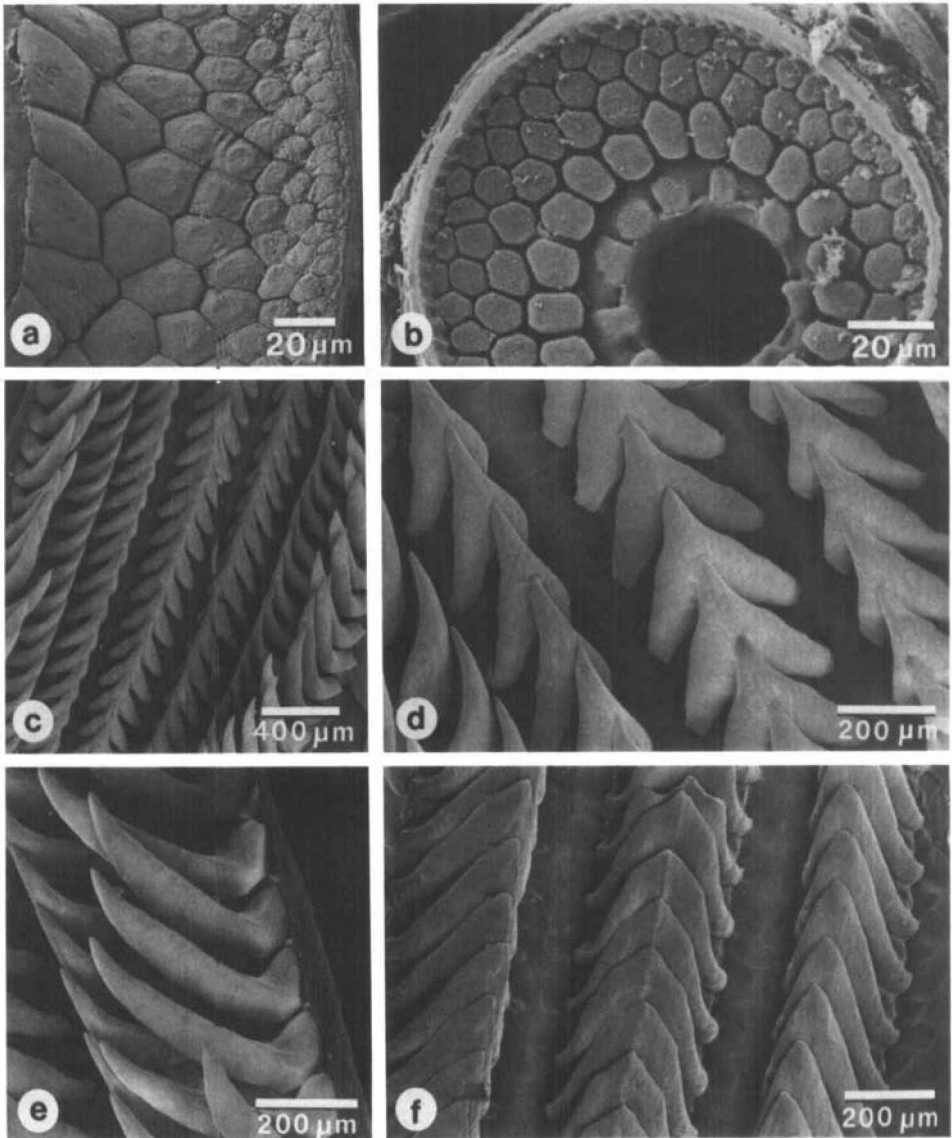
Figure 30.   *Neorossia caroli* a) arm sucker rim, male, MV F57978, 44.7 mm ML; b) club sucker rim, male, MV F57517, 38.2 mm ML; c) radula, male, MV F57978; d) radula, left to right: 2nd lateral, 1st lateral and rhachidian teeth, male, MV F57978; e) radula, right to left: 3rd lateral, 2nd lateral teeth, male, MV F57978; f) radula, left to right: 1st lateral, rhachidian teeth, female, MV F54941, 64.4 mm ML.

eye. Dorsal funnel organ; Figure 29d. Funnel locking cartilage; Figure 29e. Mantle locking cartilage; Figure 29f.

Head broader than long (mean HW/HL = 125%), slightly wider than mantle (mean HW/MW = 120%). Eyes; EDI: males, 52.74–*57.68*–63.87; females, 33.70–*51.40*–61.84. Nuchal looking cartilage; Figure 29g, NCL/NCW: males, 2.61–*3.87*–2.31; females, 1.68–*2.18*–4.00.

Arm sucker dentition; Figure 30a. Hectocotylus; Figure 29h. Proximal most
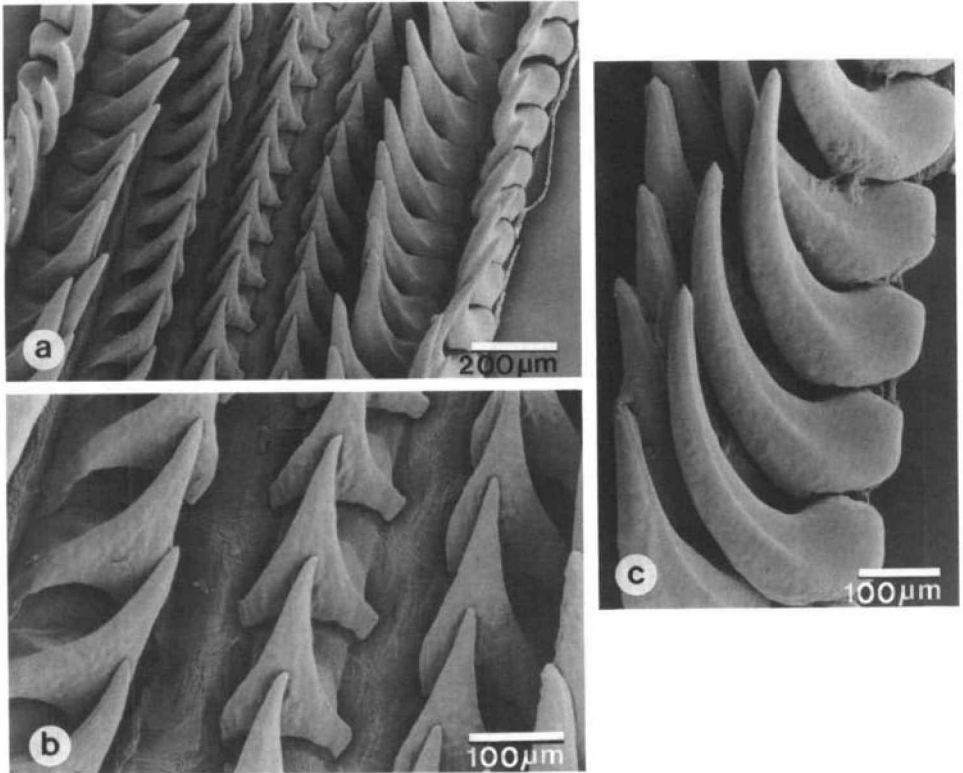
Figure 31. *Neorossia caroli* holotype, male, MOM 29-5136. a) radula; b) radula left to right: 2nd lateral, 1st lateral and rhachidian teeth; c) radula, right to left: 3rd lateral, 2nd lateral teeth.

ventral edge of arms bordered by a furrow and crest on oral surface bordered by a furrow and crest extending from sucker rows 3–18.

Tentacles relatively long and slender with naked stalks, their length ranging from approximately 1–4 times ML. Club suckers in 8–11 oblique rows. Club sucker dentition; Figure 30b. Beak; Figure 14c. Radula with seven transverse rows of teeth (Figs. 30c–f, 31a–c); rhachidian teeth very broad, stout and arrowhead-shaped without cusps, strongly indented medially at base; first lateral tooth sub-triangular, displaced toward the midline. Second and third lateral teeth with long scythe-shaped blades. Third laterals more robust and exceeding second laterals slightly in length. Base of 3rd laterals rounded. Of 3 males (mean ML 39.7 ± 4.4 mm) and 3 females (mean ML 55.8 ± 15.5 mm) the mean rhachidian tooth size was smaller in males (mean RL: males, 202.7 ± 29.1 μm; females, 272.3 ± 51.9 μm).

Digestive System (Figure 32b).—Anus with reduced anal flaps (Fig. 32c–d). In males paired epirenal bodies present, lie proximal and slightly anterior to kidney papillae (Fig. 32d).

Gladius; Figure 32e.

Reproductive System; MALES; Figure 33a.—Spermatophores; Figure 33c, d, SpLI = 36.51–*38.86*–41.22. FEMALES; Figure 33b. Ovary contains oocytes of various sizes, largest round, translucent with mean diameter 9.9 mm.
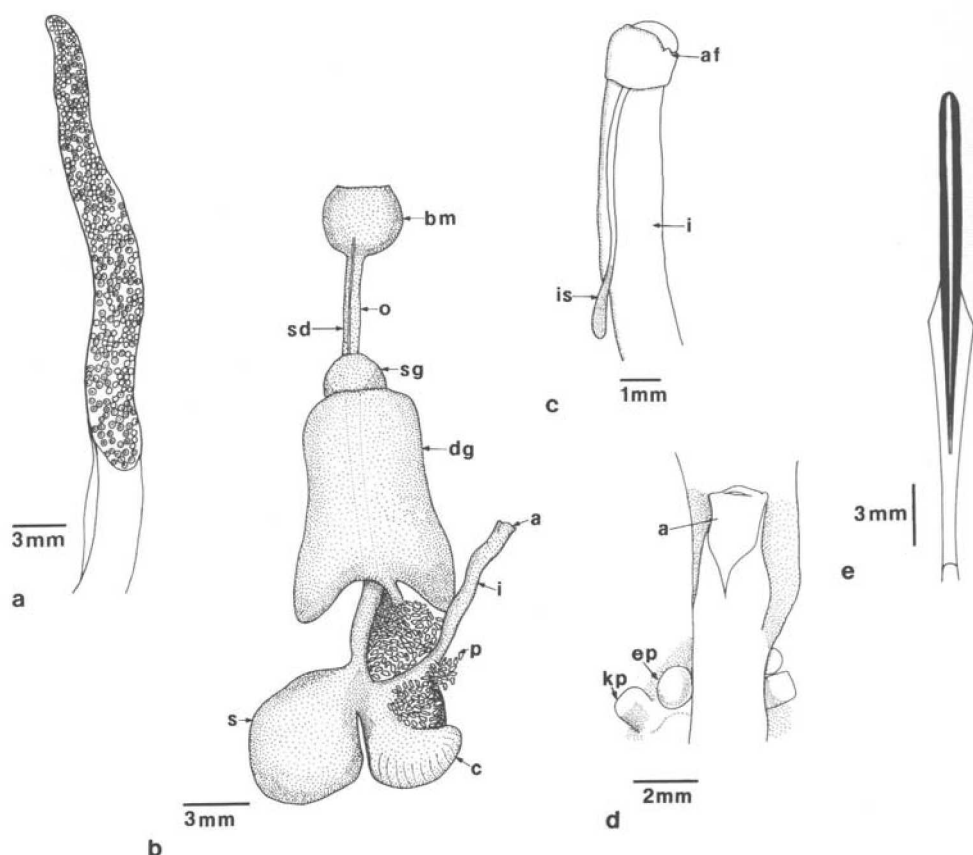
Figure 32. *Neorossia caroli* a) left tentacular club, female, MV F54939, 38.0 mm ML; b) digestive tract, ventral view, male, MV F57978, 44.7 mm ML, caecum bent back to show connection with stomach and digestive gland (a—anus, bm—buccal mass, c—caecum, dg—digestive gland, i—intestine, o—esophagus, p—pancreas, s—stomach, sd—salivary duct, sg—salivary gland); c) terminal end of intestine (af—anal flap, i—intestine, is—ink sac vestige); d) portion of anterior mantle organ complex, holotype, male, MOM 29-5136, 37.4 mm ML (a—anus, ep—epirenal body, kp—kidney papilla); e) gladius, male, MV F57978, 44.7 mm ML.

Size at Maturity.—Smallest male in which spermatophores found was 33.7 mm ML. All females larger than 62 mm ML, NDL >24.02, NDL/NDW 1.5–1.9, were mature with well-developed eggs in the ovary. Large, mature specimens have a thick gelatinous consistency.

Type Locality.—Eastern Atlantic. Azores Islands.

Distribution.—Eastern Atlantic from southwestern Iceland and Ireland to Gulf of Guinea and Mediterranean Sea, northwestern Atlantic (Nesis, 1987 in part). Namibian coast of southern Africa (this study). Distribution of material examined in this study is shown in Figure 34.

Remarks.—A single female specimen (MV F54941) was found to have an extremely peculiar tooth form not seen in any of the other material examined (Fig. 30f). This specimen did not differ in any other way from other material identified to this species and was collected from the same locality (same specimen lot) as
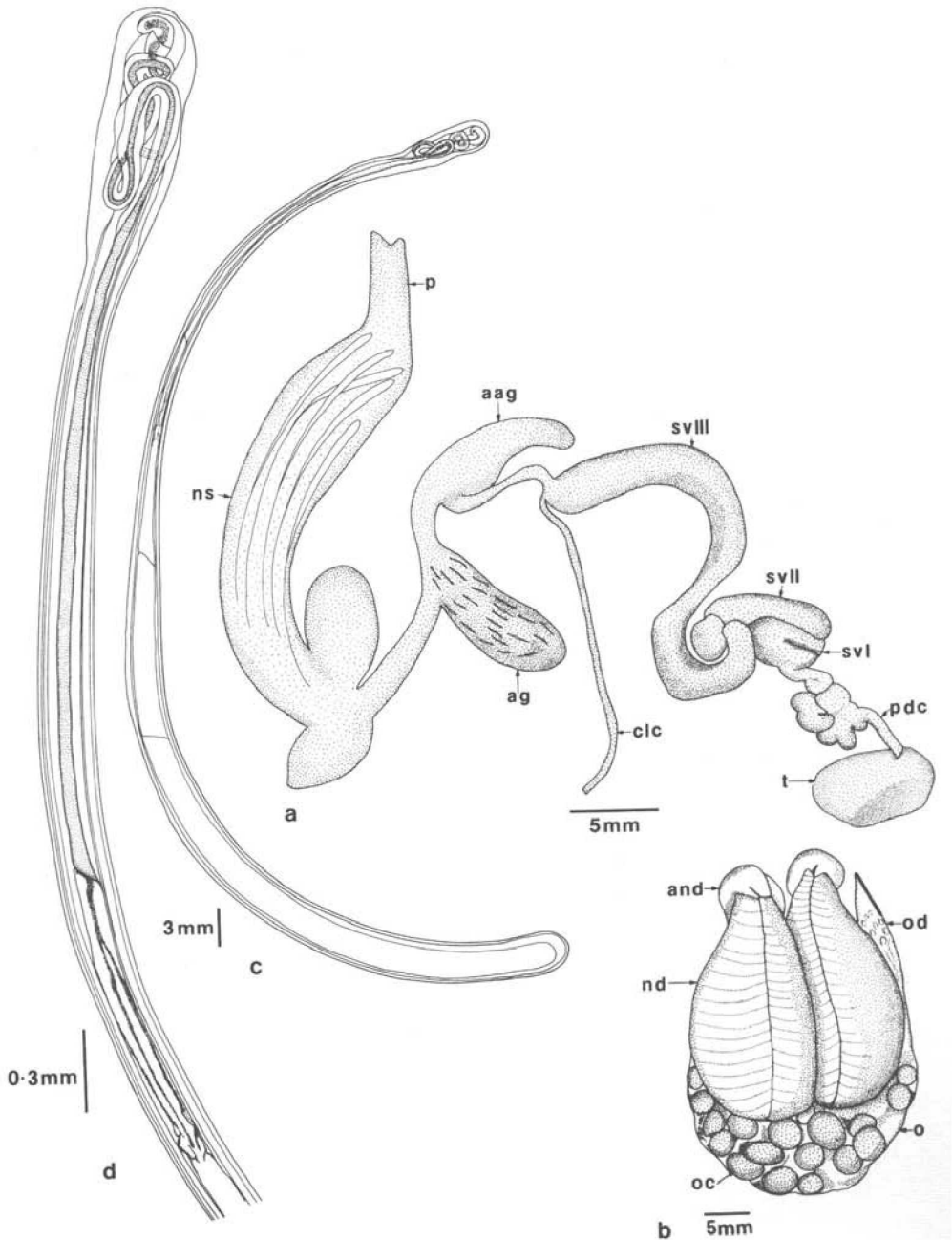
Figure 33. *Neorossia caroli* a) male reproductive organs, male, MV F57978, 44.7 mm ML (ag—accessory gland, aag—appendage of accessory gland, clc—ciliated canal, ns—Needhams sac, p—penis, pdc—proximal deferent canal, sv I–III—seminal vesicles I, II, III, t—testis); b) female reproductive organs, ventral view, MV F54941, 64.4 mm ML (and—accessory nidamental gland, nd—nidamental gland, o—ovary, oc—oocyte, od—oviduct); c) whole spermatophore, holotype, MOM 29-5136, 37.4 mm ML; d) spermatophore, oral end to sperm reservoir, holotype.
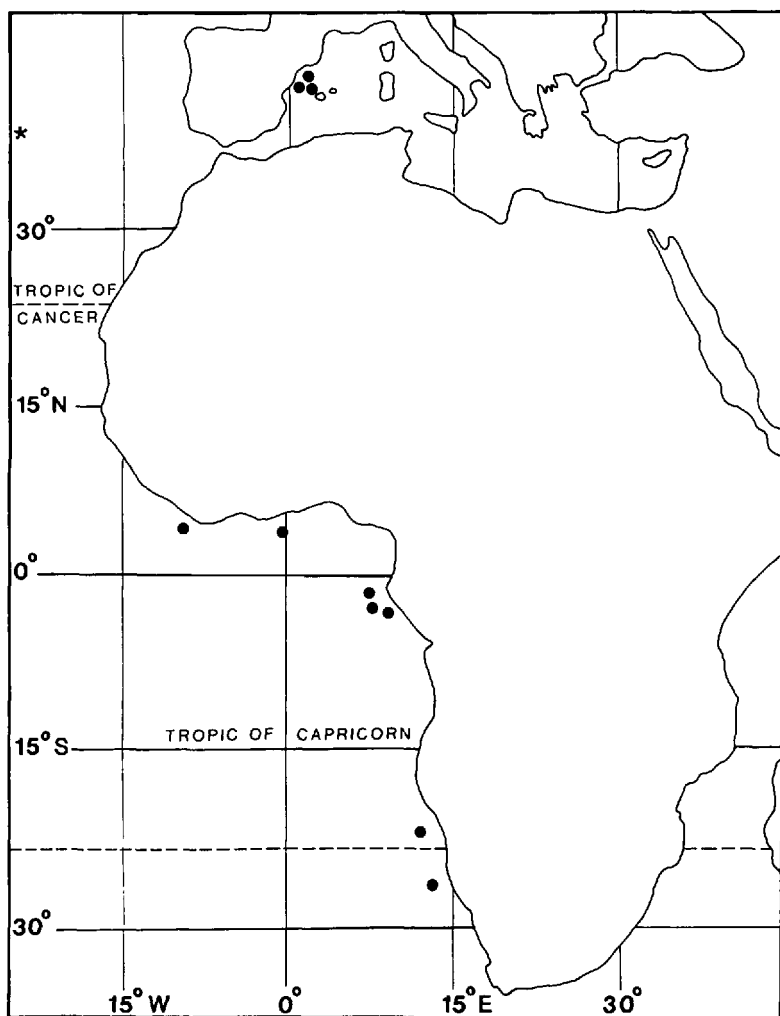
Figure 34. Distribution of *Neorossia caroli* examined in this study. Dots indicate collection sites of specimen lots, * indicates type locality.

one of the males which showed the typical tooth form. Though some slight variation was seen in the shape of teeth in other material none varied to the extent seen in this specimen.

The species was well described by Joubin (1902). Although including photographs of dorsal and ventral views, he did not include other figures. In re-examining the holotype (MOM 29-5136), a few minor differences were apparent. Joubin (1902) refers to small papillae on the epidermis of the mantle and small granules below the eye to the base of the two dorsal arms. No such papillae could be seen in this specimen or additional material examined in this study. Joubin also commented on the greatly protruding eyes. Although in other specimens the eyes are large, protruding slightly beyond the width of the mantle, the eyes of the holotype are particularly prominent. This is perhaps due to a slight dorso-ventral flattening of the head. The dorsal mantle edge is also reported to be pointed anteriorly in a marked obtuse groove. This is apparent in the holotype but variable

in other material examined and appears to be due to the extent to which the mantle is pulled away from the head during capture and preservation, an obtuse point present where the tip of the gladius supports the mantle edge. The fins and mantle of the holotype appear considerably dehydrated and possibly shrunken. The fins of other material examined are proportionally larger and more closely resemble those illustrated for *N. leptodons* n. sp., extending to the posterior end of the mantle.

Mangold-Wirz (1963) gives a detailed account of *Neorossia caroli* from the Mediterranean, providing notes on biology, reproduction, sexual maturation and comparison with other *Rossia* species. In most respects, details of the specimens examined in this study agree with those examined by Mangold-Wirz. The radula, however, is described as typical for the genus *Rossia* with "the central teeth and those on either side of the midline very long and drawn out with the ectocones well developed. The lateral teeth are slender and tapered and are contained more than twice in the length of the median teeth" (translated from p. 210). Aldrich et al. (1971) also examined the radula of a *N. caroli* male, comparing it with *R. macrosoma* Delle Chiaje, *R. pacifica* Berry, *R. tenera* Verrill and *R. sublevis* Verrill (=*R. palpebrosa* Mercer, 1968). The radula of *N. caroli* was not figured; however among these species it was decided that "no species specific variation could be determined, although there was some individual variation in rhachidian and other tooth forms" (p. 1591). In contrast, the radula has in this study proved to be a useful character by which to distinguish *N. caroli* from *N. leptodons* n. sp.

Boletzky (1971) noticed that *Neorossia caroli*, unlike any of the other Rossiinae, did not possess a well-developed ink sac and anal valves. He also refers to the prominent epirenal bodies which are present in this species and *Neorossia leptodons* n. sp.

Tables 23 and 24 give ranges, means and standard deviations of counts and indices for *Neorossia caroli* examined in this study and *Neorossia leptodons* n. sp. As can be seen in the table, ranges overlap for all characters. When further material is examined, the ratio of NCL/NCW should be checked as it may prove to be useful in distinguishing the two species. The nuchal locking cartilage is considerably broader in *N. leptodons* n. sp. males examined (with non-overlapping ranges).

Insufficient numbers of *Neorossia leptodons* n. sp. males at the time of writing precluded a comprehensive comparison of the two species; however, comparison of females using DFA supports the hypothesis that two groups are distinct species with MW, AL II, AS I and AS III weighting heavily in the formation of the function (Table 13). For meristics, ASCT II, ASCT III and ASCT IV show significant univariate differences between means; counts for each of the characters are higher for *N. caroli*.

LITERATURE CITED

Aldrich, M. M., V. C. Barber and C. J. Emerson. 1971. Scanning electron microscopical studies of some cephalopod radulae. Can. J. of Zool. 49(12): 1589–1594.

Atchley, W. R., C. T. Gaskins and D. Anderson. 1976. Statistical properties of ratios. I Emperical results. Syst. Zool. 25(2): 137–148.

Berry, S. S. 1911. Preliminary notices of some new Pacific cephalopods. Proc. U.S. Natn. Mus. 40(1838): 589–592.

———. 1912. A review of the cephalopods of western North America. Bull. Bur. Fish. Wash. 30: 269–336.

———. 1918. Report on the Cephalopoda obtained by the F.I.S. "Endeavour" in the Great Australian Bight and other southern Australian localities. Biological results of the fishing experiments carried on by the F.I.S. "Endeavour," 1909–14. 4(5): 203–298.

Boletzky, S. von. 1970. Biological results of the University of Miami deep sea expeditions 54. On the presence of light organs in Semirossia Steenstrup 1887 (Mollusca: Cephalopoda). Bull. Mar. Sci. 20: 374–388.

———. 1971. Neorossia N.G. pro Rossia (Allorossia) caroli Joubin, 1902, with remarks on the generic status of Semirossia Steenstrup, 1887. (Mollusca: Cephalopoda). Bull. Mar. Sci. 21: 964–969.

Boletzky, S. von and M. V. von Boletzky. 1973. Observations on the embryonic and early post embryonic development of Rossia macrosoma (Mollusca: Cephalopoda). Helgoländer Wiss Mee-resunters. 25: 135–161.

Brocco, S. L. 1971. Aspects of the biology of the sepiolid squid Rossia pacifica Berry. Unpublished M.Sc. Thesis, U. Victoria, Canada. 151 pp.

Chun, C. 1910, 1915. The Cephalopoda. Part I. Oegopsida. Part II. Myopsida, Octopoda. Scientific results of the German deepsea expedition on board the steamship "Valdivia" 1898–1899, Vol 18. Translated from the German. Israel Program for Scientific Translations Jerusalem 1975, 436 pp.

Clarke, M. R. 1986. Handbook for the identification of cephalopod beaks. Oxford Science Publications, New York. 273 pp.

Cotton, B. C. 1938. The Sir Joseph Banks Islands reports of the expedition of the McCoy society for field investigation and research. 5. Mollusca, Pt. 1: The spermatophore of Rossia australis Berry. Proc. R. Soc. Vict. (N.S.) 50(2): 338–340.

Cotton, B. C. and F. K. Godfrey. 1940. The molluscs of South Australia. F. Trygg, Adelaide 2: 317–600.

Joubin, L. 1902. Observations sur divers Céphalopodes Sixième note: sur une nouvelle espèce du genre Rossia. Bull. Soc. Zool. Fr. 25: 138–143.

Mangold-Wirz, K. 1963. Contribution a l'étude de Rossia caroli Joubin. Vie Milieu 14(1): 205–224.

Mercer, M. C. 1968. Systematics of the sepiolid squid Rossia Owen 1835 in Canadian waters with a preliminary review of the genus and notes on biology. Unpublished M.Sc. Thesis, Memorial University of Newfoundland, St. Johns, Canada. 96 pp.

Nei, M. 1972. Genetic distance between populations. Am. Nat. 106: 283–292.

Nesis, K. N. 1979. A brief review of zoogeography of the Australian–New Zealand pelagic realm (Cephalopoda). Trudy Inst. Okeanol. 106: 125–139.

———. 1987. Cephalopods of the world. T.F.H. Publications, Neptune City. New Jersey. 351 pp.

Nixon, M. and P. N. Dilly. 1977. Sucker surfaces and prey capture. M. Nixon and J. B. Messenger, eds. In the biology of cephalopods. Symp. Zool. Soc. Lond. 38: 447–511.

Owen, R. 1835. Mollusca–Cephalopoda. Ross appendix to the narrative of a second voyage in search of a North West Passage (J. C. Ross, ed.). 1829–1833, Appendix 2, XCII–XCIX.

Reid, A. 1990. Taxonomic review of the Australian Rossiinae (Cephalopoda: Sepiolidae). Unpublished M.Sc. Thesis, Macquarie University, Sydney, Australia. 101 pp.

Richardson, B. J., P. R. Baverstock and M. Adams. 1986. Allozyme electrophoresis. A handbook for animal systematics and population studies. Academic Press, Sydney, Australia.

Robson, G. C. 1924. On the cephalopods obtained in South African waters by Dr J. D. F. Gillchrist in 1920–21. Proc. Zool. Soc. Lond. 2: 589–686.

Roper, C. F. E. and G. L. Voss. 1983. Guidelines for taxonomic descriptions of cephalopod species. Mem. Natn. Mus. Vict. 44: 48–63.

————, M. J. Sweeney and C. E. Nauen. 1984. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO Species Catalogue 3(125): 1–227.

Sasaki, M. 1920. Report of cephalopods collected during 1906 by the United States Bureau of Fisheries Steamer "Albatross" in the Northwestern Pacific. Proc. U.S. Natn. Mus. 57: 163–203.

————. 1929. A monograph of the Dibranchiate cephalopods of the Japanese and adjacent waters, Vol. 20. Sapporo U. Press. Sapporo, Japan.

Sweeney, M. J., C. F. E. Roper and F. G. Hochberg. 1988. A catalogue of the type specimens of recent Cephalopoda described by S. Stillman Berry. Malacologia 29(1): 7–19.

Tompsett, D. H. 1939. Sepia. L.M.B.C. Mem. typ. Br. mar. Pl. Anim. 32. 1–184, pls. 1–24.

Vecchione, M., C. F. E. Roper and M. J. Sweeny. 1989. Marine flora and fauna of the eastern United States. Mollusca: Cephalopoda. NOAA Tech. Rept. NMFS 73: 23 pp.

Verrill, A. E. 1881. The cephalopods of the north-east coast of America. Part II. The smaller cephalopods including the "squids" and the octopi, with other allied forms. Trans. Conn. Acad. Arts Sci. 5(6): 259–446.

————. 1883. Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England. Brief contributions to zoology from the Museum of Yale College (No XLVII). Am. J. Sci. 20(41): 392.

Voss, G. 1955. The Cephalopoda obtained by the Harvard-Havana expedition off the coast of Cuba in 1938–39. Bull. Mar. Sci. Gulf Caribb. 5: 81–115.

————. 1956. A review of the cephalopods of the Gulf of Mexico. Bull. Mar. Sci. Gulf Caribb. 6: 90–107.

————. 1962. South African cephalopods. Trans. Royal Soc. S. Afr. 36(4): 245–272.

————. 1963. Cephalopods of the Philippine Islands. Bull. U.S. Natn. Mus. 234. 180 pp.

Winterbottom, R., J. D. Reist and C. D. Goodchild. 1984. Geographic variation in *Congrogadus subducens* (Teleostei, Perciformes, Congrogadidae). Can. J. Zool. 62: 1605–1617.

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Appendix 1a. Material examined *Rossia australis* (M = Male, F = Female, * = specimens used for electrophoresis). For distribution map showing localities listed below, see Figure 16

No.	Reg. No.	Location		Date	Depth (m)	Collector
		_°_'S	_°_'S			
Holotype						
1M	AM C148246	130°50'S	—°'S	6-vi-1913	457–548	FIS 'Endeavour' E3636
Paratype						
1F	USNM 815719	130°50'S	—°'S	6-vi-1913	457–548	FIS 'Endeavour' E3635
2F	AM C161419	144°04'E	11°35'S	12-ii-1979	420	AM FNQ 79-32
2F	MV F57449	153°54'E–153°54'E	27°16'S–27°24'S	26-ix-1982	540	'Iron Summer' Shot 6
1F	MV F57450	154°01'E	28°01'S	4-xii-1982	580	'Iron Summer' Shot 1
		154°00'E	28°00'S			
1M	MV F57451	153°48'E	26°34'S	13-xii-1982	575	'Iron Summer' Shot 2
		153°50'E	26°30'S			
2F	MV F57452	153°57'E–153°57'E	27°40'S–27°36'S	22-xi-1982	530	'Iron Summer' Shot 1
7F	MV F57453	153°55'E–153°53'E	27°18'S–27°13'S	10-v-1983	560	'Iron Summer' Shot 3
1F	MV F57454	153°22'E	27°13'S	25-iii-1983		'Iron Summer' Shot 6
7F	MV F57455	153°56'E–153°53'E	27°19'S–27°13'S	9-v-1983	590	'Iron Summer' Shot 1
5F	MV F57456	153°52'E–153°58'E	27°13'S–27°22'S	30-vii-1984	500–540	'Iron Summer'
7F	MV F57457	153°52'E–153°58'E	27°13'S–27°22'S	2-x-1982	500–540	'Iron Summer'
1F	MV F57458	153°55'E–153°53'E	27°18'S–27°14'S	31-iii-1983	620	'Iron Summer' Shot 7
1F	MV F57459	153°54'E–153°55'E	27°19'S–27°14'S	31-iii-1983	600	'Iron Summer' Shot 6
1F	MV F57460	153°54'E–153°57'E	27°15'S–27°20'S	31-iii-1983	540	'Iron Summer' Shot 5
3F	MV F57461	153°54'E–153°54'E	27°14'S–27°19'S	24-ix-1982	535	'Iron Summer' Shot 2
3F	MV F57480	153°53,47'E	27°19.9'S	10-v-1983	600	'Iron Summer' Shot 2
6F	MV F57462	153°55'E–153°55'E	27°22'S–27°19'S	5-xii-1982	570	'Iron Summer' Shot 4
3F	MV F57463	153°55'E–153°56'E	27°39'S–27°34'S	24-iii-1983	540	'Iron Summer' Shot 4
3F	MV F57464	153°58'E–153°57'E	27°41'S–27°35'S	31-iii-1983	540	'Iron Summer' Shot 3
3F	MV F57465	153°57'E–153°57'E	27°37'S–27°36'S	31-iii-1983	520	'Iron Summer' Shot 4
3F	AM C161420	154°00'E–154°00'E	28°01'S–27°58'E	17-viii-1987	550	FRV 'Kapala' K78-17-10
1F	AM C161421	153°56'E–153°56'E	28°08'S–28°05'S	1-vi-1978	410–411	KRV 'Kapala' K78-0902
1F	AM C161422	153°47'E–153°48'E	29°26'S–29°22'S	12-x-1978	256–274	KRV 'Kapala' K75-09-07
12F	AM C161423	153°43'E–153°43'E	29°52'S–29°51'S	23-viii-1977	500–512	KRV 'Kapala' K77-13-10
2F	AM C161424	153°41'E–153°43'E	29°57'S–29°49'S	10-x-1975	452–457	KRV 'Kapala' K75-09-02
1F	AM C161425	153°26'E	30°20'S	22-viii-1977	267–274	KRV 'Kapala' K77-13-07
10F	AM C161426	152°42'E–152°41'E	32°50'S–32°52'S	6-xii-1987	550	KRV 'Kapala' K78-26-11
3F	AM C100759	152°31'E–152°26'E	33°02'S–33°06'S	18-viii-1975	457	KRV 'Kapala' K75-05-03
1F	AM C161427	152°31'E–152°26'E	33°02'S–33°06'S	18-viii-1975	457	KRV 'Kapala' K75-05-03

Appendix 1a.   Continued

No.		Reg. No.	Location	Date	Depth (m)	Collector
1F	1M	AM C161428	33°18'S 151°32'E	viii-1979	400	KRV 'Kapala' K79-12-07
1F		MV F57466	33°31.7'S–33°28.7'S 127°15'E–127°19'E	28-ii-1976	640–650	KN Nesis
2F		AM C161429	33°32'S–33°35'S 152°02'E–152°00'E	21-viii-1979	366	FRV 'Kapala' K79-12-08
1F		AM C161430	33°32'S–33°47'S 151°50'E–152°02'E	5-x-1972	503	FRV 'Kapala' K72-05-25
6F	1M	AM C161431	33°33'S–33°36'S 151°02'E–151°01'E	5-xii-1979	439	FRV 'Kapala' K79-20-09
3F		MV F57467	33°36'S 152°00'E	24-i-1982	624–632	FV 'Soela' S01/82/44
2F		AM C161432	33°36'S–33°44'S 151°57'E–151°52'E	13-x-1976	384	FRV 'Kapala' K76-16-02/3
2F		AM C161433	33°37'S–33°34'S 151°56'E–151°57'E	7-xii-1978	542	FRV 'Kapala' K78-26-18
1F		MV F57468	33°38'S–33°23'S 127°93'E–127°59'E	28-iii-1979	415–420	FV 'Courageous' 47-1020
6F	1M	MV F57469	33°39'S 151°52'E	25-i-1983	410–420	FV 'Soela' S01/82
5F	1M	AM C81690	33°40'S–33°51'S 152°45'E–152°54'E	13-17-iv-1981	475–503	FRV 'Kapala' K71-06-04
4F		MV F51382	33°41'S 151°53'E	24-i-1982	632–640	FV 'Soela' S01/82
2F		AM C161434	33°41'S–33°33'S 151°55'E–152°03'E	20-24-iv-1971	549	FRV 'Kapala' K71-07-01
4F		AM C161435	33°42'S–33°39'S 151°51'E–151°53'E	5-xii-1979	450–457	FRV 'Kapala' K79-20-11
29F	3M	AM C105864	33°42'S–33°39'S 151°52'E–151°54'E	20-xii-1976	448–460	FRV 'Kapala' K76-24-01
1F		MV F57470	33°43'S 151°52'E	25-i-1982	420	FV 'Soela' S01/82/47
1F		MV F57471	33°43'S 151°55'E	25-i-1982	560–620	FV 'Soela' S01/82/23
1F		MV F57472	33°46'S–33°44'S 151°49'E–151°50'E	9-ix-1981	414–499	FRV 'Kapala' K81-17-03
12F	1M	MV F57473	33°46'S–33°44'S 151°49'E–151°50'E	9-ix-1981	414–499	FRV 'Kapala' K81-17-03
3F		MV F57474	33°47'S 151°48'E	24-i-1982	420–440	FV 'Soela' S01/82/42
1F	1M	MV F57475	33°49'S–33°49'S 151°33'E–151°34'E	9-ix-1981	130–133	FRV 'Kapala' K81-17-02
1F		AM C161436	33°42'S 151°52'E	6-iv-1971	274	FRV 'Kapala' K71-05-03
*3F		AM C161437	34°14'S–34°17'S 151°29'E–151°26'E	28-vii-1987	375–430	FRV 'Kapala' K87-13-02
4F		AM C161438	34°18'S–34°24'S 151°26'E–151°21'E	20-viii-1975	457–484	FRV 'Kapala' K75-05-06
1F		AM C161439	34°19'13"S 151°24'28"E	28-vi-1971	366	FRV 'Kapala' K71-10-03
44F	7M	AM C161440	34°21'S–34°19'S 151°23'E–151°25'E	13-xii-1978	439	FRV 'Kapala' K78-27-13
1F		AM C161441	34°22'S–34°19'S 151°23'E–151°25'E	14-xii-1978	439	FRV 'Kapala' K78-27-16
1F	1M	AM C161442	34°26'S–34°18'S 151°21'E–151°25'E	20-vi-1975	457	FRV 'Kapala' K75-02-14
1F		AM C161443	34°28'S–34°34'S 151°19'E–151°17'E	20-viii-1975	411	FRV 'Kapala' K75-05-07
2F		AM C161444	34°36'S–34°45'S 151°16'E–151°13'E	21-viii-1975	503	FRV 'Kapala' K75-05-08
1F		AM C161445	34°40'S–35°01'S 151°07'E–151°13'E	25-v-1971	366–549	FRV 'Kapala' K71-11-06/07
	2M	MV F57479	34°43.55'S–34°43.74'S 151°13.16'E–151°12.21'E	22-x-1988	345–450	RV 'Franklin' Stn. 57
32F		AM C161446	34°54'S–34°57'S 151°12'E–151°11'E	12-xii-1978	550	FRV 'Kapala' K78-27-06
	1M	AM C161447	35°00'S–34°54'S 151°06'E–151°08'E	6-vii-1977	337	FRV 'Kapala' K77-09-03
4F		AM C161448	35°01'S–34°58'S 151°07'E–151°08'E	4-xii-1980	457	FRV 'Kapala' K80-19-06

Appendix 1a. Continued

No.	Reg. No.	Location	Date	Depth (m)	Collector
1F	AM C161449	35°31'S–35°36'S 150°46'E–150°43'E	24-xi-1976	439	FRV 'Kapala' K76-21-03/5
1F	AM C161450	35°32'S–35°35'S 150°46'E–150°44'E	22-xi-1977	503	FRV 'Kapala' K77-21-05
*1F	AM C161452	37°12'S–37°12'S 138°36'E–138°33'E	7-ii-1989	603–622	MSL 07-38
2F 1M	AM C161453	37°39'S–37°45'S 150°17'E–150°13'E	30-vii-1971	403–408	FRV 'Kapala' K71-11-02
1F	MV F57476	37°41.5'S 150°14'E	4-ii-1985	458	FV 'Soela' S01/85/45
1F	AM C161454	37°42'S–37°39'S 150°16'E–150°17'E	30-vii-1971	393	FRV 'Kapala' K71-13-01
2F	MV F57477	37°45.2'S 150°13.4'E	28-xi-1984	426–430	FV 'Soela' S06/84/13
1F	MV F57478	38°01.7'S 150°04.9'E	3-iii-1985	400	FV 'Soela' S01/85/42
2F	MV F57481	38°09.1'S 149°54'E	3-iii-1985	444	FV 'Soela' S01/85/41
5F	MV F51885	38°13'S–38°14'S 150°05'E–149°40'E	4-v-1984	464–472	FV 'Soela' S02/84/70
1F	MV F57482	39°01.4'S 148°38.7'E	6-iii-1985	660–670	FV 'Soela' S01/85/53
1F	MV F52378	39°04.4'S 148°38.8'E	29-xi-1984	448	FV 'Soela' S06/84/16
1M	MV F57483	39°20.5'S 148°46.3'E	2-ii-1985	440	FV 'Soela' S01/85/38
1F	MV F57484	39°03.9'S 148°39'E	30-x-1984	432–460	FV 'Soela' S05/84/21
		Western Tasmania			
1F	MV F57485	40°41'S–40°39'S 143°31'E–143°31'E	16-i-1982	1,190	'Challenger' TFDA
*4F 1M	AM C161455	41°15'S 144°08'E	2-ii-1989	520	MSL 07-24
1F	MV F57486	41°05.1'S 143°56.3'E	20-x-1984	520	FV 'Soela' S05/84/51
1F	MV F57487	41°02.5'S 143°53.1'E	27-i-1985	360	FV 'Soela' S01/85/16
1F	MV F57488	40°59.2'S 143°50.4'E	27-i-1985	518–520	FV 'Soela' S01/85/17
1M	MV F57489	40°27.6'S 143°23.6'E	31-i-1985	540–542	FV 'Soela' S01/85/25
1F	MV F57490	38°50'S–38°50'S 141°46'E–141°55'E	28-i-1985	578	FV 'Soela' S01/85/20
2F	MV F30329	38°50'S–38°51'S 141°46'E–141°55'E	5-iii-1980	288	—
1F	MV F57491	38°50'S–38°51'S 141°46'E–141°55'E	5-iv-1980	540	'Halcyon'
1M	MV F30330	38°50'S–38°51'S 141°46'E–141°55'E	6-iii-1980	540	'Halcyon'
2M	MV F57492	38°50'S–38°51'S 141°46'E–141°55'E	6-iii-1980	540	'Halcyon' 80/3
1F	MV F30325	38°34'S 141°04'E	5-iii-1980	540	'Halcyon' MFG 13
4F	MV F58847	38°34'S 141°04'E	4-iii-1980	540	'Halcyon'
1M	MV F57975	38°31'S–38°34'S 140°57'E–141°00'E	4-iii-1980	540	RV 'Sarda'
1F	SAM D18687		14-v-1981	603	'Wendy Bell'

Appendix 1b. Material examined *Rossia* sp. 1 (M = Male, F = Female, * = specimens used for electrophoresis). For distribution map showing the localities listed below, see Figure 22

No.	Reg. No.	Location	Date	Depth (m)	Collector
1F	WAM 966.87	18°40'S–18°40'S 117°13'E–117°11'E	13-iv-1982	396–398	FV 'Soela' S02/82/43
1F	MV F57495	18°35'S 117°29'E	31-i-1984	404	FV 'Soela' S01/84/22
1F	MV F57496	18°34'S–18°36'S 117°27'E–117°23'E	16-viii-1983	400–402	FV 'Soela' S04/83/90
1M	MV F58424	18°30'S 117°34'E	9-ii-1989	380	FV 'Courageous'
1M	MV F57494	18°20'S 117°50'E	—	430	—
1F	AM C161418	18°08'S 118°11'E	27-i-1984	360	FV 'Soela' S01/84/1
1F	MV F57497	18°08'S 118°05'E	2-ii-1984	448	FV 'Soela' S01/84/26
1F	MV F57498	17°57'S 118°18'E	17-iv-1984	450	FV 'Soela' S01/84/3
2F	MV F54923	17°26'S 118°52'E	3-ix-1988	425	FV 'Surefire'
1F	MV F57499	17°17'S 120°12'E	4-ii-1984	304	FV 'Soela' S01/84/39
2F	MV F49424	17°17'S 119°00'E	2-ix-1988	455	FV 'Surefire'
2F	MV F57500	17°10'S 119°10'E	2-ix-1988	455	FV 'Surefire'
2F	WAM 967.87	16°58.7'S–16°56.6'S 119°55.6'E–119°56.6'E	9-ii-1984	430–432	FV 'Soela' S01/84/49
1M	WAM 977.87	16°57'S–16°55'S 119°51'E–119°54'E	22-ii-1984	436	FV 'Soela' S01/84/113
1F	WAM 975.87	16°55.8'S–17°01.8'S 119°53.9'E–119°51.3'E	19-ii-1984	426	FV 'Soela' S01/84/96
1M	WAM 978.87	16°55.4'S–16°57.4'S 119°52.3'E–119°46.4'E	23-ii-1984	436–448	FV 'Soela' S01/84/116
1F	WAM 976.87	16°55.2'S–16°54.1'S 119°52.8'E–119°54.8'E	20-ii-1984	430–432	FV 'Soela' S01/84/102
1M	WAM 968.87	16°41.8'S–16°40.5'S 120°07.3'E–120°09.7'E	9-ii-1984	430–434	FV 'Soela' S01/84/50
4M	WAM 970.87	15°48.0'S–15°50.1'S 120°41.0'E–120°39.5'E	10-ii-1984	396–400	FV 'Soela' S01/84/53
1M	WAM 969.87	15°46.4'S–15°43.8'S 120°39.9'E–120°39.8'E	10-ii-1984	446–450	FV 'Soela' S01/84/52
1M	WAM 971.87	15°12.8'S–15°10.4'S 121°05.9'E–121°09.2'E	11-ii-1984	404–410	FV 'Soela' S01/84/58
1F	WAM 972.87	14°50.2'S–14°48.6'S 121°31.4'E–121°33.2'E	12-ii-1984	356	FV 'Soela' S01/84/64
1F	WAM 979.87	13°50.3'S–13°53.4'S 122°18.5'E–122°16.7'E	13-ii-1982	450–452	FV 'Soela' S01/84/71
2F	WAM 973.87	13°33.3'S–13°34.3'S 122°54.5'E–122°52.3'E	14-ii-1984	390–394	FV 'Soela' S01/84/77
1M	WAM 444.72	13°28.3'S 123°09.7'E	23-xii-1969	370	'Umitaki Maru' Stn 6910
1F	WAM 974.87	13°27.6'S–13°25.0'S 122°44.4'E–122°47.0'E	14-ii-1984	440–444	FV 'Soela' S01/84/78
2F	MV F57501	NW Shelf	28-xi-1983		FV 'Soela' S01/83/1

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Appendix 1c. Material examined *Rossia mastigophora.* For distribution map showing localities listed below, see Appendix 2

No.		Reg. No.	Location		Date	Depth (m)	Collector
3F		USNM 814055	25°29'S	33°35'E	28-ix-1964	450	RV 'Anton Bruun' 396C
7F		MV F57519	29°38'S	14°54'E	26-i-1989	335	'Benguela XIV' Survey
1F	1M	MV F57518	30°21'5"S	15°46'2"E	22-ii-1988		RV 'Africana' 'Chicha Touza' 51
1F	2M	USNM 814056	02°50'S	40°31'E	8-xi-1964	290	RV 'Anton Bruun' 421-H
1F		USNM 814057	02°56'S	40°28'E	8-xi-1964	240	RV 'Anton Bruun' 421-G
1F	1M	MV F57976	30°21'5"S	15°46'2"E	22-ii-1988	245	RV 'Africana'

Appendix 1d. Material examined *Neorossia leptodons* n. sp. (M = Males, F = Females, * = specimens used for electrophoresis). For distribution map showing the localities listed below, see Figure 28

No.	Reg. No.	Location		Date	Depth (m)	Collector
Holotype						
1M	MV F57504	37°18.81'S–37°17.76'S	138°36.3'E–138°35.01'E	28-i-1988	980–1,060	FV 'Soela' S01/88/27
1F	AM C161456	32°08'S	153°07'E	12-xi-1983	915–951	FRV 'Kapala' K83-15-01
1F	AM C161457	33°32'S–33°38'S	152°00'E–152°04'E	9-viii-1975	823	FRV 'Kapala' K75-05-05
1F	AM C161458	33°39'S–33°37'S	152°06'E–152°07'E	6-xii-1979	1,000	FRV 'Kapala' K79-20-15
1F	AM C161459	34°00'S	151°43'E	6-xi-1972	731	FRV 'Kapala' K07-01
1M	AM C161460	34°51'S–34°55'S	151°15'E–151°14'E	26-x-1983	1,026–1,035	FRV 'Kapala' K83-14-05
1F	AM C161461	35°26'S–34°55'S	150°56'E–150°53'E	1-i-1984	1,062–1,098	FRV 'Kapala' K84-11-07
1F	AM C161462	35°30'S	151°52'E	3-iv-1984	933–979	FRV 'Kapala' K84-04-01
1F	MV F57502	36°56.48'S–36°57.35'S	137°21.87'E–137°27.05'E	24-i-1988	920–950	FV 'Soela' S01/88/4
1M	AM C161465	37°12'S–37°12'S	138°36'E–138°33'E	7-ii-1989	603–622	MSL 07/38
1F	MV F57503	37°18.25'S–37°17.7'S	138°39.52'E–138°37.04'E	27-i-1988	800–840	FV 'Soela' S01/88/25
*1M	AM C161463	37°20'S–37°20'S	138°45'E–138°42'E	7-ii-1989	979	MSL 07/35
1M	MV F30324	38°31'S	141°04'E	4-iii-1980	540	FV 'Halcyon'
1F	MV F57505	38°34'S	141°04'E	4-iii-1980	540	FV 'Halcyon'
2M	MV F58425	40°27.6'S	143°23.6'E	28-i-1985	560	FV 'Soela' S01/85/20
*1F	AM C161464	40°45'S–40°46'S	143°31'E–143°32'E	2-ii-1989	942	MSL 07/22
1F	MV F57506	40°59.2'S	143°50.4'E	31-i-1985	540–542	FV 'Soela' S01/85/25
1F	MV F57507	41°32.3'S	144°22.2'E	29-i-1985	538–556	FV 'Soela' S01/85/23
1F	MV F57515	41°48'S–41°43.7'S	144°26'E–144°23.7'E	16-v-1986	992–1,000	FV 'Soela' S03/86/32
1F	MV F57515	41°48'S–41°43.7'S	144°26'E	16-v-1986	992–1,000	FV 'Soela' S03/86/32
1F	MV F57515	41°48'S–41°43.7'S	144°26'E–144°23.7'E	16-v-1986	992–1,000	FV 'Soela' S03/86/32
1F	MV F57516	42°18.3'S	144°39'E	9-vii-1983	1,110	TFDA 6/9
1F	MV F52341	44°04'S–44°03.6'S	146°24.2'E–146°21.3'E	11-v-1984	504–528	FV 'Soela' S02/84/94
1F	SAM D18632	33°42'S	132°25'E	12-viii-1989	130	FV 'Merindah Pearl'
1F	SAM D18724	33°58'S	131°22'E	xi-1989	1,000	FV 'Saxon Progress'
1M	SAM D18725	33°58'S	131°22'E	xi-1989	1,000	FV 'Saxon Progress'
3M	SAM D18726	33°58'S	131°22'E	xi-1989	1,000	FV 'Saxon Progress'

Appendix 1e. *Neorossia caroli* (M = Male, F = Female). For distribution map showing the localities listed below, see Figure 34

No.	Reg. No.	Location		Date	Depth (m)	Collector
Holotype						
1M	MOM 29-5136	Near Azores Is.		12-vii-1901	1,098	'Princess Alice' 1118
1M	MV F54940	41°11'N	02°27'E	10-vii-1988	1,069	'Marinovich'
1F	MV F54941	41°11'N	02°27'E	10-vii-1988	1,069	'Marinovich'
1F	MV F54942	39°30'N	02°15'E	9-viii-1988	580–620	
1F	UMML 31.779	04°40'N	09°20'W	4-vii-1964	366	'Pillsbury' P-73
1F	UMML 31.1163	04°12'N	04°28'E	26-v-1965		'Pillsbury' P-309
1F	UMML 31.2070	02°30'S	08°52'E	5-ix-1963	549	RV 'Geronimo' 2-214
2F	USNM 816879	02°30'S	08°52'E	5-ix-1963	40	RV 'Geronimo' 2-214
1M	USNM 816878	03°05'S	09°15'E	6-ix-1963	40	RV 'Geronimo' 2-223
1F	MV F54939	23°23'S	13°00'E	25-vii-1988	622	'Chicha Touza' 106-25
1F	MV F57977	Off Banyuls-sur-mer		16-ii-1972		
1M	MV F57978	Off Banyuls-sur-mer		16-ii-1972		
1M	MV F57517	Golfo de Cadiz, Spain		18-x-1988		
1M	UMML 31.1164	Bou-Haroun Algere Chalut par le travers de Castiglione		vii-1955	500–700	
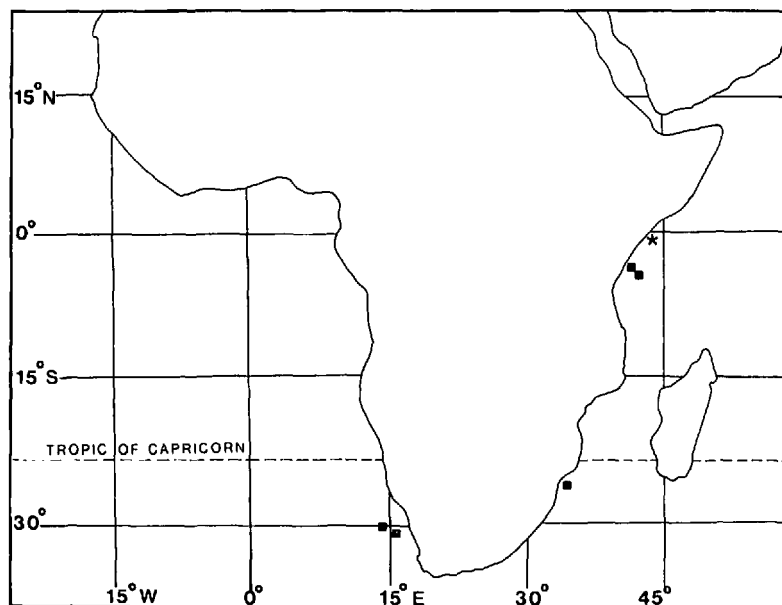
Appendix 2.   Southern African distribution of *R. mastigophora* examined in this study. Solid squares indicate specimen lots. * indicates type locality.

Appendix 3a.   Australian *Rossia* males and females. Regression equations used to calculate residuals ($Y = a + bML$) where Y = predicted value of that dependent variable, a = intercept, b = slope, Sig. = significance of regression model: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, r^2 = variance proportion explained by that model

Dep. variable	Males				Females			
	r^2	a	b	Sig.	r^2	a	b	Sig.
MW	0.498	−0.65	0.667	***	0.570	3.85	0.593	***
HL	0.519	2.76	0.589	***	0.577	5.71	0.491	***
HW	0.300	8.64	0.467	***	0.539	12.21	0.428	***
ED	0.132	5.91	0.296	**	0.466	10.29	0.257	***
NCL	0.626	0.53	0.193	***	0.537	2.13	0.163	***
NCW	0.306	0.78	0.046	***	0.410	0.75	0.053	***
FuL	0.224	4.01	0.303	***	0.592	1.52	0.340	***
AL I	0.550	0.32	1.046	***	0.563	7.38	0.674	***
AL II	0.490	0.41	1.162	***	0.631	8.98	0.732	***
AL III	0.518	−0.98	1.221	***	0.621	9.80	0.755	***
AL IV	0.471	4.00	0.931	***	0.641	7.99	0.716	***
CIL	0.172	−0.58	0.732	*	0.266	7.09	0.588	***
AS I	0.162	0.44	0.031	**	0.301	0.91	0.014	***
AS II	0.372	0.22	0.071	***	0.302	1.05	0.017	***
AS III	0.399	0.16	0.072	***	0.384	1.01	0.019	***
AS IV	0.253	0.39	0.057	***	0.409	0.91	0.013	***
FP	0.343	0.40	0.176	***	0.399	−0.71	0.181	***
FI	0.731	1.53	0.505	***	0.780	2.03	0.525	***
FL	0.669	4.05	0.572	***	0.766	3.76	0.620	***
FWS	0.540	2.52	0.326	***	0.596	2.26	0.357	***
FWT	0.640	6.42	1.133	***	0.761	8.63	1.180	***

Appendix 3b.   Australian *Rossia* males and females, North West Shelf specimens excluded. Regression equations used to calculate residuals ($Y = a + bML$) where Y = predicted value of that dependent variable, a = intercept, b = slope, Sig. = significance of regression model: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant, r^2 = variance proportion explained by that model

Dep. variable	Males				Females			
	r^2	a	b	Sig.	r^2	a	b	Sig.
MW	0.383	1.08	0.609	***	0.527	6.09	0.532	***
HL	0.347	5.74	0.480	***	0.532	7.19	0.447	***
HW	0.154	13.55	0.323	*	0.529	1.76	0.174	***
ED	0.016	11.74	0.107	N/S	0.513	9.05	0.291	***
NCL	0.593	1.34	0.170	***	0.529	1.76	0.174	***
NCW	0.328	0.64	0.053	***	0.411	0.56	0.057	***
FuL	0.134	4.85	0.265	*	0.562	3.10	0.293	***
AL I	0.496	1.27	1.026	***	0.489	10.59	0.583	***
AL II	0.380	1.47	1.142	***	0.548	11.03	0.672	***
AL III	0.356	3.83	1.069	***	0.577	12.12	0.689	***
AL IV	0.337	7.60	0.834	***	0.623	9.19	0.675	***
CIL	0.252	2.01	0.563	*	0.164	16.71	0.324	***
AS I	0.139	0.48	0.033	*	0.312	0.87	0.015	***
AS II	0.534	0.21	0.077	***	0.310	0.96	0.018	***
AS III	0.425	0.33	0.073	***	0.369	0.98	0.020	***
AS IV	0.335	0.68	0.053	***	0.460	0.84	0.015	***
FP	0.240	0.59	0.163	***	0.318	0.19	0.155	***
FI	0.675	0.97	0.522	***	0.750	2.41	0.512	***
FL	0.630	2.64	0.625	***	0.717	4.64	0.594	***
FWS	0.407	3.61	0.288	***	0.529	3.18	0.330	***
FWT	0.461	12.58	0.925	***	0.721	11.20	0.721	***

Appendix 3c. Australian *Rossia* Group 1 and *Rossia mastigophora* males and females. Regression equations used to calculate residuals ($Y = a + bML$) where Y = predicted value of that dependent variable, a = intercept, b = slope, Sig. = significance of regression model: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant, r^2 = variance proportion explained by that model

Dep. variable	Males				Females			
	r^2	a	b	Sig.	r^2	a	b	Sig.
MW	0.527	0.05	0.615	***	0.571	0.78	0.677	***
HL	0.685	0.66	0.649	***	0.512	6.68	0.489	***
HW	0.734	0.06	0.709	***	0.444	14.58	0.353	***
ED	0.684	−1.71	0.528	***	0.523	10.62	0.215	***
NCL	0.755	−1.30	0.238	***	0.700	1.82	0.162	***
NCW	0.576	0.18	0.062	***	0.440	1.15	0.045	***
FuL	0.329	5.73	0.260	*	0.546	3.67	0.334	***
AL I	0.610	−1.23	1.041	***	0.625	6.01	0.750	***
AL II	0.763	1.59	1.063	***	0.661	13.55	0.664	***
AL III	0.697	−4.92	1.289	***	0.610	10.95	0.767	***
AL IV	0.749	−0.23	0.971	***	0.438	15.83	0.580	***
CIL	0.192	19.67	0.292	N/S	0.178	11.64	0.601	**
AS I	0.359	0.11	0.038	**	0.103	1.30	0.007	N/S
AS II	0.619	−0.50	0.084	***	0.183	1.44	0.008	*
AS III	0.583	−0.80	0.094	***	0.356	1.27	0.015	***
AS IV	0.538	−0.43	0.071	**	0.137	1.11	0.008	N/S
FP	0.397	−0.38	0.353	**	0.475	0.50	0.178	***
FI	0.855	2.48	0.482	***	0.824	5.91	0.472	***
FL	0.782	6.01	0.496	***	0.839	6.78	0.588	***
FWS	0.579	2.39	0.330	***	0.617	5.21	0.316	***
FWT	0.730	5.13	1.137	***	0.828	10.92	1.201	***

Appendix 3d. Australian *Rossia* Group 2 and *R. mastigophora* males and females. Regression equations used to calculate residuals ($Y = a + bML$) where Y = predicted value of that dependent variable, a = intercept, b = slope, Sig. = significance of regression model: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant, r^2 = variance proportion explained by that model

Dep. variable	Males				Females			
	r^2	a	b	Sig.	r^2	a	b	Sig.
MW	0.296	4.31	0.486	***	0.528	6.35	0.524	***
HL	0.342	6.61	0.444	***	0.521	7.84	0.428	***
HW	0.192	13.42	0.329	**	0.520	12.21	0.426	***
ED	0.042	10.50	0.155	N/S	0.494	9.51	0.278	***
NCL	0.492	1.62	0.157	***	0.553	1.66	0.176	***
NCW	0.425	0.40	0.062	***	0.438	0.48	0.060	***
FuL	0.132	5.58	0.238	*	0.567	3.17	0.292	***
AL I	0.444	4.21	0.911	***	0.492	10.95	0.572	***
AL II	0.345	5.30	0.995	***	0.543	12.09	0.643	***
AL III	0.303	7.93	0.913	***	0.587	12.40	0.682	***
AL IV	0.234	12.82	0.629	***	0.603	10.44	0.641	***
CIL	0.383	−3.79	0.791	***	0.147	16.85	0.316	***
AS I	0.103	0.67	0.027	*	0.299	0.88	0.014	***
AS II	0.434	0.50	0.067	***	0.293	1.01	0.017	***
AS III	0.392	0.45	0.069	***	0.368	0.99	0.020	***
AS IV	0.228	0.98	0.042	***	0.420	0.86	0.014	***
FP	0.366	−4.70	0.362	***	0.328	0.23	0.154	***
FI	0.726	0.69	0.532	***	0.754	2.42	0.514	***
FL	0.629	3.79	0.582	***	0.720	4.66	0.596	***
FWS	0.361	4.28	0.265	***	0.521	3.64	0.319	***
FWT	0.195	0.96	1.250	**	0.734	10.63	1.121	***

Appendix 3e. Australian *Neorossia* and *N. caroli* males and females. Regression equations used to calculate residuals ($Y = a + bML$) where Y = predicted value of that dependent variable, a = intercept, b = slope, Sig. = significance of regression model: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N/S = not significant, r^2 = variance proportion explained by that model

Dep. variable	Males				Females			
	r^2	a	b	Sig.	r^2	a	b	Sig.
MW	0.703	2.70	0.689	***	0.874	4.97	0.657	***
HL	0.828	−0.22	0.732	***	0.901	5.73	0.556	***
HW	0.508	4.81	0.803	*	0.771	12.69	0.548	***
ED	0.743	−0.18	0.574	***	0.790	6.87	0.334	***
NCL	0.806	−1.51	0.247	***	0.923	1.25	0.167	***
NCW	0.484	0.49	0.094	*	0.815	0.21	0.109	***
FuL	0.822	2.07	0.410	***	0.846	3.12	0.403	***
AL I	0.484	5.56	0.701	**	0.830	6.24	0.706	***
AL II	0.761	−2.49	1.063	***	0.920	4.05	0.858	***
AL III	0.489	6.02	0.952	*	0.907	5.09	0.954	***
AL IV	0.694	−2.96	1.068	**	0.887	6.52	0.829	***
CIL	0.017	15.84	0.088	N/S	0.644	8.81	0.426	***
AS I	0.393	0.37	0.031	N/S	0.635	0.73	0.019	***
AS II	0.553	0.14	0.050	**	0.668	0.81	0.023	***
AS III	0.429	0.64	0.039	*	0.671	0.84	0.024	***
AS IV	0.646	0.09	0.047	**	0.729	0.54	0.024	***
FP	0.592	−0.27	0.187	**	0.591	2.03	0.124	***
FI	0.630	0.36	0.554	**	0.933	−1.67	0.658	***
FL	0.494	1.18	0.603	*	0.891	0.26	0.727	***
FWS	0.060	5.62	0.193	N/S	0.821	−1.38	0.450	***
FWT	0.483	19.32	0.840	*	0.881	7.08	1.332	***
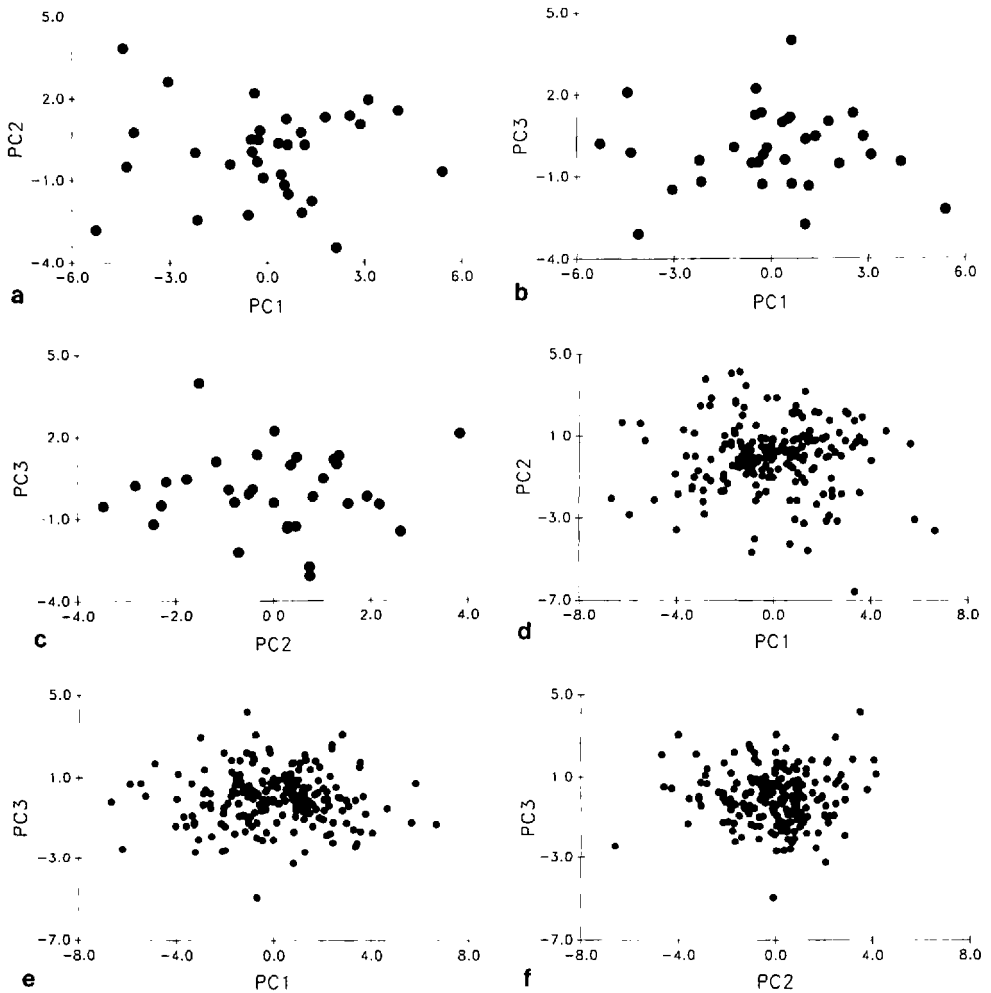
Appendix 4-1. Scatter plots of first three PCA scores. a)–c) Australian *Rossia* males (excluding North West Shelf specimens); d)–f) Australian *Rossia* females (excluding North West Shelf specimens. a) and d) PC1 vs. PC2, b) and e) PC1 vs. PC3, c) and f) PC2 vs. PC3. Percent variance accounted for by the first three principal components for males: PC1 22.1%, PC2 12.9% and PC3 10.1% and females: PC1 23.3%, PC2 13.1% and PC3 8.0%.
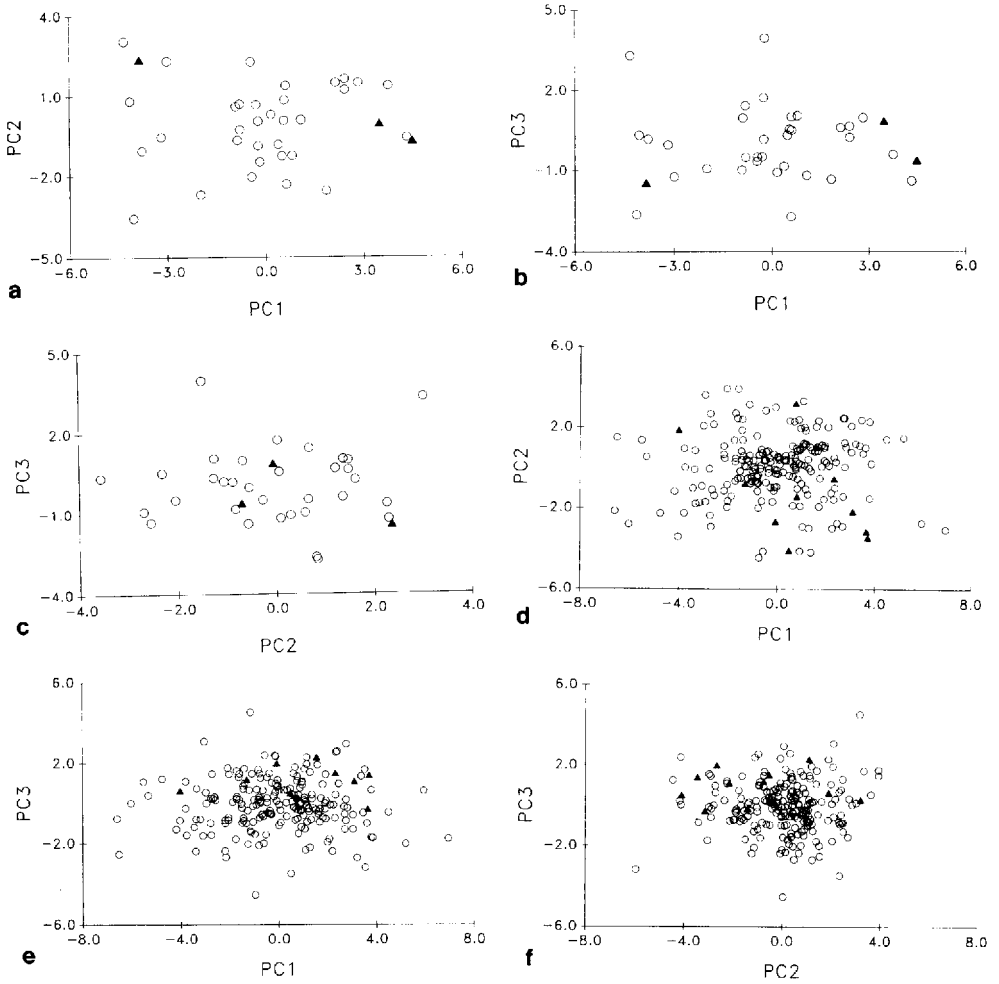
Appendix 4-2.   Scatter plots of the first three PCA scores. a)–c) Group 2 and *R. mastigophora* males, d)–f) Group 2, and *R. mastigophora* females. a) and d) PC1 vs. PC2, b) and e) PC1 vs. PC3, c) and f) PC2 vs. PC3. Open circles = Group 2, solid triangles = *R. mastigophora*. Percent variance accounted for by the first three principal components for males: PC1 29.3%, PC2 12.2% and PC3 9.5% and females: PC1 23.3%, PC2 13.4% and PC3 7.8%.
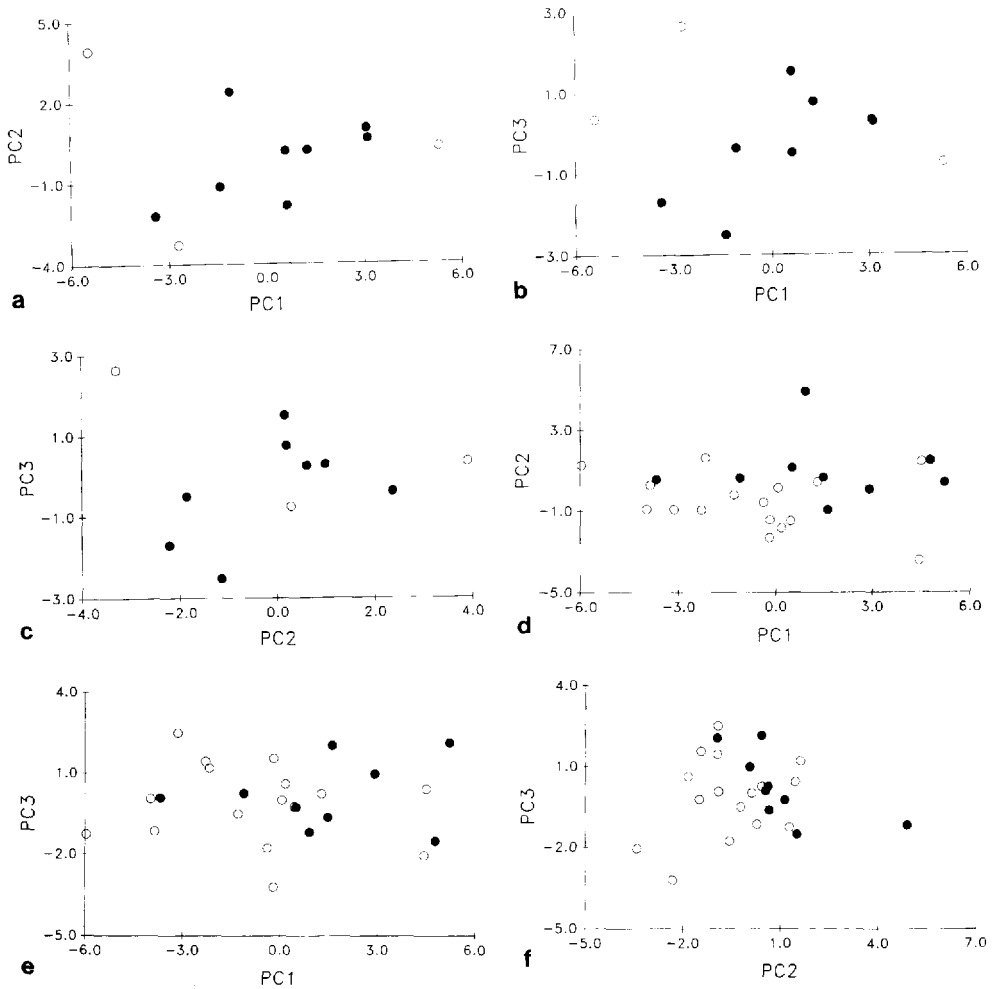
Appendix 4-3.   Scatter plots of the first three PCA scores. a)–c) Australian *Neorossia* and *N. caroli* males, Australian *Neorossia* and *N. caroli* females. a) and d) PC1 vs. PC2, b) and e) PC1 vs. PC3, c) and f) PC2 vs. PC3. Open circles = Australian *Neorossia,* solid circles = *N. caroli*. Percent variance accounted for by the first three principal components for males: PC1 48.6%, PC2 19.2%, PC3 9.7% and females: PC1 41.4%, PC2 12.8%, and PC3 9.4%.

Appendix 5. Selected characters of *Rossia* (*Rossia*) species. Abbreviations: M = males, F = females, AP = anal pads, EP = epirenal bodies, P = present, A = absent, WD = well developed, R = reduced. Symbols: + = club not expanded, * = club moderately expanded, *** = club expanded. 'Other' includes potentially diagnostic features (not always available for all species). N.B. Characters should be treated with caution pending a full revision of the genus

Species	Source	Club sucker rows	Epirenal bodies/ anal pads	Arm suckers
R. brachyura Verrill 1883	Voss, 1955	16 / *	??/??	4 rows medially / 2 distally
R. bullisi Voss 1956	Voss, 1956 / Mercer, 1968 / Boletzky, 1970 / Boletzky, 1971 / Roper et al., 1984	10–13 / very small uniform size*	P M, A F/A / M, A F	2 rows, apertures rounded, larger in males
R. macrosoma (Delle Chiaje 1829)	Boletzky, 1971 / Boletzky and Boletzky, 1973 / Roper et al., 1984	8–12 / subequal denticulate, web borders entire club***	A M, A F/A / M, A F	2–4 medially / 2 distally, outer rows enlarged, greatly reduced toward tips
R. megaptera Verrill 1881	Mangold-Wirz, 1963 / Mercer, 1968 / Boletzky, 1971 / Vecchione et al., 1989	6–7 / flattened orally / +	P M, A / F/?, A F	2 rows denticulate, larger in males, uniform size throughout
R. moelleri Steenstrup 1856	Mercer, 1968 / Boletzky, 1971	3–4 proximally, 3–6 distally, subequal-blunt denticulate, club suckers larger than arm suckers**	A M, A F/ / A M, A F	2 rows (sometimes 2–3 irregular), larger in males, small aperture
R. mollicella Sasaki 1920	Sasaki, 1920 / Sasaki, 1929 / Mercer, 1968 / Boletzky, 1971	4–10 / subequal denticulate, large proximally / +	A M, A F/ / A M, A F	2 rows (sometimes 2–3 irregular) slitlike aperture
R. pacifica Berry 1911	Berry, 1911 / Sasaki, 1929 / Mercer, 1968 / Brocco, 1971 / Roper et al., 1984	6–8 proximally / 4 distally / subequal, blunt denticulate; club flattened orally, web borders entire club**	A M, A F/ / A M, A F	2 rows (often 3–4 medially), larger in males, apertures often slitlike
R. pacifica diegensis Berry 1912	Berry, 1912	2–4 medially, denticulate	P M, A F/ / A M, A F	2 rows
R. palpebrosa Owen 1834	Mercer, 1968 / Vecchione et al., 1989	6–10 / subequal denticulate**	A M, A F/ / A M, A F	2 rows females, 3–4 rows males; larger in males
R. tortugaensis Voss 1956	Voss, 1956 / Boletzky, 1971 / Roper et al., 1984	6–10 / denticulate +	A M, A F/ / A M, A F	2 rows, suckers often barrel shaped, oval apertures

Appendix 5. Continued

Species	Anal flaps/ink sac	Hectocotylus	Other	Distribution
R. brachyura Verrill 1883	WD/WD	?	Funnel organ short squat; arms deep webbed	U.S.A. east coast
R. bullisi Voss 1956	WD/WD	GC entire arm length	Funnel organ dorsal pad with narrow extensions	Northern Gulf of Mexico
R. macrosoma (Delle Chiaje, 1829)	WD/WD	GC ½ arm length; suckers 4 rows medially, 2 rows distally and proximally	Arms III and IV deep web; nuchal cartilage broad, oval; beak without tooth	East Atlantic / North Sea / Norway, Britain / Mediterranean / Azores-West Africa
R. megaptera Verrill 1881	R/WD	GC entire arm length; suckers smaller than sessile arms	Funnel organ strongly shouldered, dorsal pad with long extensions	West Atlantic / Hudson Canyon / Davis Strait / West Greenland
R. moelleri Steenstrup 1856	WD/WD	Thick GC bordered by membrane—rows 3–17; suckers smaller than sessile arms	Funnel organ square fleshy ridged shoulders	Northeastern Canada / West Greenland / N.E. Greenland / Spitzbergen / Jan Mayen and Kara Seas
R. mollicella Sasaki 1920	WD/WD	GC rows 2–14 ? entire	Ventral mantle > dorsal nuchal cartilage narrow ovate	Kii Province / Japan
R. pacifica Berry 1911	WD/WD	GC double membrane ⅔ arm length, suckers smaller than sessile arms, biserial; nuchal cartilage narrow, ovoid	Funnel organ shouldered; lower beak with tooth on shoulder	Neretic North Pacific and Japan / Aleutian Islands and North America to 32°N
R. pacifica diegensis Berry 1912	WD/WD	GC entire		California
R. palpebrosa Owen 1834	WD/WD	GC entire arm length, suckers smaller than sessile arms	Arm IV with keel, funnel organ, blunt posteriorly; papillae on dorsal head and mantle	Greenland and the Canadian Arctic to south Carolina in western Atlantic from Spitzbergen to North sea in eastern Atlantic
R. tortugaensis Voss 1956	R/WD	GC entire arm length	Arms long	Gulf of Mexico